NAVIGATING THE PREDATOR GAUNTLET: CONSUMPTION OF HATCHERY- AND WILD-BORN JUVENILE CHUM SALMON (*ONCORHYNCHUS KETA*) BY COMMON NEARSHORE MARINE FISHES IN SOUTHEAST ALASKA

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Douglas H. Duncan, B.A.

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APPROVED:

Dr. Anne H. Beaudreau, Committee Chair
Dr. Megan V. McPhee, Committee Member
Dr. Peter A. H. Westley, Committee Member
Milo D. Adkison, Chair
Department of Fisheries
S. Bradley Moran, Dean
College of Fisheries and Ocean Sciences
Michael Castellini
Dean of the Graduate School

Abstract

Juvenile chum salmon (*Oncorhynchus keta*) undergo extensive mortality at marine entry, a period which is believed to be a potential population bottleneck. Although this early mortality has been consistently observed, our understanding of the mechanisms responsible is limited. Furthermore, the implications of large-scale salmon hatchery releases for the ecology of juvenile chum salmon and their consumers is another important knowledge gap. To better understand the predation responses of abundant consumers to hatchery- and wild-born juvenile chum salmon, we examined the diets of Pacific staghorn sculpin (*Leptocottus armatus*) and Dolly Varden (*Salvelinus malma*) near Juneau, Alaska, in 2016 and 2017. Chum salmon composed 4.5% and 19.6% of the diets of staghorn sculpin and Dolly Varden by weight, respectively, and 88% of chum salmon individuals consumed were of hatchery origin. Chum salmon prey were shorter than average when compared to chum salmon concurrently collected by beach seine and hatchery releases of chum salmon. Regression analyses indicated that occurrence of juvenile chum salmon in diets varied primarily by date and site. Predation generally occurred more frequently at sites closer to hatchery release areas. The quantity of chum salmon in staghorn sculpin stomachs was related to predator length, chum salmon catch-per-unit-effort (CPUE), and the proportion of hatchery fish present; however, date was the only important predictor explaining quantity of chum salmon in Dolly Varden stomachs. To translate diet data into consumption rate, we experimentally determined gastric evacuation rate for staghorn sculpin and implemented a field-based consumption model. Average daily consumption of chum salmon was low relative to all other prey groups. Estimates of average seasonal consumption of juvenile chum salmon by staghorn sculpins suggest that predator populations would have to be implausibly large to consume even 1% of local hatchery chum salmon production. Together,

these results yield new insights into the interactions between the predators of wild-born and hatchery-born salmon during the critical stage of marine entry.

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General Introduction

Estuary habitats are profoundly important for a wide range of commercially and ecologically important fish and invertebrate species. An estuary is defined by Day (1980) as "a partially enclosed coastal body of water which is either permanently or periodically open to the sea and within which there is a measurable variation of salinity due to the mixture of sea water with freshwater derived from land drainage…" Estuaries are a transition from freshwater systems to the marine environment and possess a diverse range of microhabitats, salinities, temperatures, and other conditions that provide essential habitat and migratory pathways for many different organisms (Beck et al. 2001).

Anadromous salmon (*Oncorhynchus* spp.) are economically, culturally, and ecologically important fishes that use estuary habitats around the northern Pacific rim. Returning adults move through estuaries on their homeward spawning migrations into streams, rivers, and lakes. Juvenile salmon migrate out of freshwater and, depending on the species, spend a varying amount of time in estuaries physiologically adapting to saltwater and feeding before moving further offshore (Morita et al. 2005). Healthy estuaries provide juvenile salmon with favorable growing conditions and refuge from predators, which can increase survival (Magnusson & Hilborn 2003). Despite these advantages, marine entry is still one of the most dangerous periods for salmon, with many studies finding evidence for extensive mortality at this stage (Bax 1983, Healey 1982, Ricker 1976). While many coastal species have been shown to consume juvenile salmon, salmon are often a minority of their overall diet compositions (Beamish et al. 1992, Orsi et al. 2000, Whitney et al. 2017). No specific single predator, group of predators, or other mortality source have been consistently implicated as the mechanism responsible for high rates of mortality on juvenile salmon in estuaries (Cross et al. 2009).

To better assess the effects of predation mortality on salmon population dynamics, more knowledge is required about the diets of predators that interact with juvenile salmon in nearshore habitats (Hillgruber & Zimmerman 2009). In addition, information on predator consumption rates and population sizes is required to determine the scope of impact that any one predator group may have on juvenile salmon abundances. While it is unrealistic to assess the impact of most commercially unimportant predators on juvenile salmon in a single study, building the information required for such exercises, including diet information and physiological rates, allows for estimates to be generated when data are available. Continuing to evaluate predation at this stage is essential because early marine mortality has been found to be a major driver in salmon population variability (Beamish & Mahnken 2001).

Patterns of early marine mortality in salmon are likely altered and potentially obscured by large scale enhancement programs, which in Southeast Alaska release approximately 600 million juvenile salmon into the nearshore marine environment each year (Stopha 2017). These releases, consisting primarily of chum salmon (*O. keta*), serve to increase harvest in regional common property fisheries, but also constitute a major input of potential prey that may attract predators to hatchery release areas (Beamish et al. 1992, Brannon et al. 2004). High abundances of hatchery salmon could reduce predation on wild-born salmon through predator buffering (Willette et al. 2001, Briscoe et al. 2005). Alternatively, predator aggregation could potentially intensify predation mortality for wild-born salmon through apparent competition. Understanding how and when hatchery releases might mediate predation on wild-born salmon stocks is of interest to hatchery operators and salmon mangers in Alaska. Identifying the conditions in which hatchery releases may increase or reduce predation on wild-born salmon, and whether predators exhibit

preference for either hatchery- or wild-born salmon are key components to more fully understanding the ecological implications of hatchery activity.

This thesis evaluated the use of hatchery- and wild-born juvenile chum salmon by two common predators at four estuary sites along Lynn Canal, Southeast Alaska, in 2016 and 2017. The first focal predator, Pacific staghorn sculpin (*Leptocottus armatus*), is known to consume juvenile salmon (Mace 1983, Whitney et al. 2017) and staghorn sculpins are common occupants of salmon-bearing estuaries, from California to Alaska. The ubiquity of staghorn sculpins in many nearshore systems has generated interest in their food habits in the southern portions of their range (Mace 1983, Armstrong 1991), but with the exception of Whitney et al. (2017), their feeding ecology remains poorly described in Alaska. The second focal predator, Dolly Varden (*Salvelinus malma*), also overlaps in estuaries with juvenile salmon. Dolly Varden are associated with salmon at multiple life stages and are well documented to consume salmon eggs, salmon fry, and salmon smolts, but with high variation across time and space (Armstrong & Bond 2013, Armstrong 1970, Roos 1959). A modern assessment of staghorn sculpin and Dolly Varden use of juvenile salmon in estuaries will begin to address knowledge gaps, including the proportion of salmon in their diets, spatiotemporal variability in salmon consumption, ecological factors influencing consumption, and size-selectivity.

The first chapter of this thesis focused on quantifying the diet compositions and patterns of predation on juvenile chum salmon for both predators. Our objectives were to (1) quantify the contribution of juvenile chum salmon prey to diets of staghorn sculpin and Dolly Varden in Southeast Alaska estuaries, (2) determine size- and origin-based relationships between predators and salmon prey, (3) characterize spatial and temporal patterns in predation on hatchery- and wild-born smolts, and (4) evaluate the relative importance of time, location, predator size, and

prey characteristics in explaining variation in predation on juvenile salmon. A combination of field sampling, assessment of predator stomach contents, and hatchery release data provided new information about the use of juvenile chum salmon, and its variation, by two ubiquitous estuarine predators.

The second chapter scaled up diet data to mass-specific consumption rate for staghorn sculpins. To develop a tool for estimating the overall consumption demand of staghorn sculpin on juvenile salmon, we sought to 1) experimentally determine gastric evacuation rate of staghorn sculpin and use the results to parameterize a field-based consumption model, 2) evaluate the field-based model estimates with a regression-based approach for back-calculating prey consumption, and 3) use the model to estimate seasonal consumption rates of salmon smolts by staghorn sculpin near Juneau, Alaska, USA. The resultant model serves as a tool that can be applied by future researchers investigating the ecological role of staghorn sculpins as an abundant estuary consumer. Overall, this thesis provides more insight into the ecological mechanisms underpinning juvenile salmon mortality and patterns of vulnerability during the critical early marine phase.

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Chapter 1: Patterns of predation on hatchery- and wild-born juvenile salmon by two abundant nearshore fishes in Southeast Alaska[1]

Abstract

Juvenile Pacific salmon (*Oncorhynchus* spp.) experience high mortality at marine entry, yet our quantitative understanding of predation during this critical period is limited. We evaluated spatial, temporal, and size-based patterns of predation on hatchery- and wild-born juvenile chum salmon (*O. keta*) by two abundant predators in Southeast Alaska estuaries, Pacific staghorn sculpin (*Leptocottus armatus*) and Dolly Varden (*Salvelinus malma*). Chum salmon comprised 4.5% of staghorn sculpin (n = 937) and 19.6% of Dolly Varden (n = 448) diets by weight, with 88% originating from hatcheries. Variation in occurrence of chum salmon in diets was driven by date and site. The quantity of chum salmon consumed by staghorn sculpins varied with predator length, chum salmon catch-per-unit-effort, and the proportion of hatchery fish present; however, date was the only important predictor for Dolly Varden. The mean length of chum salmon in diets was significantly shorter than concurrent hatchery releases or seine catches, suggesting size-selection favoring large individuals. This pattern suggests that hatchery strategies of releasing larger individuals may reduce vulnerability to estuarine predators, but trade-offs may occur later in the chum salmon life history that could offset this early size advantage.

[1] Duncan, D. H. & Beaudreau, A.H. (2018). Patterns of predation on hatchery- and wild-born juvenile salmon by two abundant nearshore fishes in Southeast Alaska. Manuscript in preparation for submission to the Canadian Journal of Fisheries and Aquatic Sciences.

Introduction

Pacific salmon (*Oncorhynchus* spp.) experience variability in year-class strength that can be linked to a range of environmental and ecological factors in their early life history. A well accepted critical period occurs as salmon enter marine waters and are subject to intensive predation (Parker 1968, Beamish and Mahnken 2001). A salmon cohort can experience up to 85% mortality during this nearshore period, which often represents the single largest component of marine mortality in the salmon life cycle (Ricker 1976, Quinn 2005). The importance of early marine predation is widely acknowledged and has motivated previous studies examining predators on juvenile salmon, including harbor seals (Yurk and Trites 2000), sea birds (Simenstad et al. 1979, Scheel and Hough 1997), and a variety of fishes (Mace 1983, Beamish et al. 1992, Orsi et al. 2000). However, information is limited on temporal, spatial, and size-based patterns of predation on juvenile salmon, particularly by nearshore fishes that may contribute substantially to mortality during estuarine rearing (Healey 1982, Bax 1983).

Assessing the vulnerability of juvenile salmon to nearshore consumers first requires knowledge of the spatial and temporal overlap between predators and potential prey. From April to June, juvenile salmon are abundant in estuaries and adjacent habitats as they leave fresh water (Groot and Margolis 1991, Quinn 2005). During nearshore marine residency, juvenile salmon are small (25-200 mm FL; Quinn 2005) which makes them susceptible to consumers of many species and sizes (Parker 1971, Hargreaves and Lebrasseur 1985, Sogard 1997, Furey et al. 2014). Given their high energy content (Anthony et al. 2000) and potentially high densities during the period of marine entry, juvenile salmon may serve as a particularly beneficial source of post-winter nutrition to nearshore consumers. In salmon stocks, early marine mortality can

drive variability in the number of returning adults (Groot and Margolis 1991, LaCroix et al. 2009).

In Alaska, hatcheries release approximately 1.4 billion juvenile Pacific salmon each year, which may artificially increase juvenile salmon densities in estuaries during beyond levels observed in a system of natural production. Elevated abundances of juvenile salmon may serve as a potential attractant to predators or source of predator population growth. Across Southeast Alaska, hatcheries currently release more than 500 million juvenile chum salmon (*O. keta*) into the nearshore environment annually, which in 2017 constituted 83% of total regional chum salmon harvests (Stopha 2017). In Southeast Alaska, as well as other regions with hatchery production, there is interest in better understanding how consumers respond to abundant juvenile hatchery salmon and if co-occurring wild-born salmon may be experiencing altered patterns of predation as a result. The increase in salmon prey abundance, and often density, driven by numerically large hatchery salmon releases are thought to increase the proportion of salmon in predator diets (Buchanan et al. 1981, Mather 1998). In some instances, hatchery releases have been shown to attract more predators or increased predation rates relative to areas of natural salmon production (Beamish et al. 1992, Brannon et al. 2004, Chenoweth et al. 2017). However, the net impact on salmon mortality is uncertain, as other studies have indicated that large releases of hatchery salmon could reduce overall predation on co-occurring wild-born salmon through predator buffering or swamping (Willette et al. 2001, Briscoe et al. 2005).

The size structure, spatial distribution, and behavior of juvenile hatchery salmon differ substantially from their wild-born counterparts, which can result in differential predation on hatchery- and wild-born salmon (Hargreaves and Lebrasseur 1985, Wertheimer and Thrower 2007, Duffy and Beauchamp 2008). For example, hatchery fish are fed in captivity and thus

released larger than wild-born individuals at marine entry (Olla et al. 1998, Sturdevant et al. 2012). This is thought to confer a survival advantage because fish predators frequently consume smaller individuals due to limitations in gape width and ease of capture (Parker 1971, Healey 1982, Sogard 1997, Olla et al. 1998). Additionally, the larger hatchery fish may migrate offshore more rapidly, which could limit their duration of overlap with nearshore predators (Healey 1982, Orsi et al. 2004, Sturdevant et al. 2012). Quantifying size-based relationships between nearshore consumers and their juvenile salmon prey is important because size-selective predation at the juvenile stage can influence the number of returning adults (Parker 1968, Ricker 1976, Beamish and Mahnken 2001, LaCroix et al. 2009).

Understanding the responses of nearshore predators to hatchery releases and their contribution to juvenile salmon mortality requires quantitative information about spatial, temporal, and size-based patterns of predation on hatchery- and wild-born salmon. Here, we focused on two abundant consumers—Pacific staghorn sculpin (*Leptocottus armatus*; hereafter staghorn sculpin) and Dolly Varden (*Salvelinus malma*)—that are commonly found in estuaries along the northeastern coast of the Pacific Ocean and have been observed to prey on juvenile salmon (Lagler and Wright 1962, Robert 1965, Armstrong 1970, Whitney et al. 2017, Whitney et al. 2018). Mace (1983) examined predation on juvenile salmon by staghorn sculpins and concluded that under certain circumstances, they had the potential to consume 5% of juvenile chum salmon and more than 42% of juvenile coho salmon (*O. kisutch*) outmigrating from the Big Qualicum River on Vancouver Island, B.C. In a 2014 study from the Juneau area, Whitney et al. (2017) found that juvenile salmon constituted 9.1% of staghorn sculpin diet by weight between April and September. The second predator, Dolly Varden, are well documented salmon egg consumers in freshwater spawning habitats (e.g., Denton et al. 2010, Armstrong and Bond

2013) and prey upon juvenile salmon in nearshore marine ecosystems (Robert 1965; Whitney et al. 2018). A study in Hanus Bay, Southeast Alaska, showed that 28% of Dolly Varden diet by volume was composed of juvenile salmon and that 22% of the Dolly Varden sampled had consumed juvenile pink or chum salmon (Armstrong 1965). However, Roos (1959) found that juvenile sockeye salmon made up 9.0% of the diet by weight and only occurred in 4.2% of sampled Dolly Varden near Chignik, Alaska. This documented variability in the use of juvenile salmon prey by both staghorn sculpin and Dolly Varden suggests that anticipating their responses to changes in prey resources requires an understanding of how patterns in their diets vary with environmental and ecological factors.

The objectives of our study were to (1) quantify the contribution of juvenile chum salmon prey to diets of staghorn sculpin and Dolly Varden in Southeast Alaska estuaries, (2) determine size- and origin-based relationships between predators and chum salmon prey, (3) characterize spatial and temporal patterns in predation on hatchery- and wild-born chum salmon, and (4) evaluate the relative importance of time, location, predator size, and prey characteristics in explaining variation in predation on juvenile salmon. We hypothesized that the quantity and sizes of salmon consumed would increase with predator size and that predators would show size-selective predation favoring smaller individuals due to increased predator avoidance ability or behaviors in larger individuals. Additionally, we expected that the contribution of juvenile salmon to predator diets would be greatest in proximity to hatchery release areas and increase with local salmon density. We focused on predation of chum salmon, which in a typical year constitute close to 50% of the value in Southeast Alaska salmon harvests, with more than half of the harvested chum salmon originating from hatcheries (McDowell Group 2010, Alaska Department of Fish and Game 2017). Better understanding the ecological responses of predators

to hatchery releases is important for hatchery operators who want to optimize enhancement strategies and for resource managers who must work to conserve co-occurring wild-born stocks.

Methods

Study area

The study was conducted in 2016 and 2017 at four estuaries (i.e., intertidal sites at river deltas) along Lynn Canal, near Juneau, Alaska, USA: Sheep Creek estuary (58.26 °N, -134.33 °W), Eagle River estuary (58.53 °N, -134.85 °W), Mendenhall River estuary (58.33 °N, -134.61 °W), and Cowee Creek estuary (58.68 °N, -134.95 °W; Figure 1). The Douglas Island Pink and Chum, Inc. (DIPAC) Macaulay Salmon Hatchery releases around 130 million salmon juvenile salmon each year, with >98% consisting of chum salmon (Stopha 2016, Stopha 2017). Hatchery salmon were released from net pens located at multiple sites near Juneau (Figure 1) between late April and early June, with most releases occurring in May of 2016 and June of 2017 (A. Zaleski, personal communication, 18 April 2018); this coincides with the general period of outmigration for wild-born salmon (Sturdevant et al. 2012). Our study sites were positioned along a gradient of distances from the hatchery chum salmon release sites. The shortest water-connected distances from each study site to the nearest hatchery release site are as follows: Sheep Creek estuary, 0.2 km; Eagle River estuary, 6.5 km; Mendenhall River estuary, 10.5 km; and Cowee Creek estuary, 15.5 km (Figure 1).

Sample collection

We conducted fieldwork from May to July of 2016 and April to July of 2017. Sampling occurred after hatchery chum salmon releases began, due to an unexpected early release of hatchery fish, but before most fish were released in 2016, and both before and after all hatchery

releases in 2017. All sites were sampled twice per month through July and monthly in August and September (Table 1). Juvenile salmon and focal predators were primarily collected with beach seines. All seining was conducted within two hours of negative low tides during morning daylight hours following Whitney et al. (2017). Habitat type was consistent across sites, made up of shallow sloping sand or mud with occasional patches of exposed cobble (Whitney et al. 2017). We used two 15.2 m long x 2.4 m deep seine nets, each with a different mesh size (0.95 cm and 1.27 cm stretched knotless mesh), with the goal of capturing as wide a range of fish species and sizes as feasible. On each sampling day, we conducted 4-8 alternating sets using the two seines. Small, narrow-bodied fishes, including some juvenile salmon, were able to escape through the mesh; therefore, when juvenile salmon were captured, we conducted an additional set with a smaller mesh seine (10 m long x 2.4 m wide net with 0.64 cm stretched knotless mesh) to increase our sample size of juvenile salmon for determining length distributions and proportions of hatchery- and wild born salmon. Given the capability for large Dolly Varden to avoid beach seines, we opportunistically used hook-and-line sampling at the study sites between seine sampling days to capture larger-bodied Dolly Varden.

Fish from each set were identified, counted, and measured; when more than 50 individuals of a species were captured, we haphazardly sampled a representative 50 individuals to measure for length. Up to 30 staghorn sculpins and 30 Dolly Varden with sufficient mouth gape to consume fish (Whitney 2016) were haphazardly sampled from multiple seine sets during each sampling event (day x site), euthanized, and retained for stomach content analysis. These sample sizes were adequate to characterize diversity in diets, based on previous research on these species in Juneau-area estuaries (Whitney et al. 2017, Whitney et al. 2018). Up to 30 juvenile chum salmon captured in beach seines were also haphazardly retained from multiple seine sets

during each sampling event to determine the length distributions and proportions of hatchery- and wild-born chum salmon present. Additionally, 30 juvenile chum salmon provided by Macaulay from each net pen were haphazardly selected and measured to assess size frequency at release.

Laboratory analysis

Stomach content analysis was conducted in accordance with previous diet studies (e.g., Beaudreau and Essington 2007, Whitney et al. 2017). Briefly, retained predators were measured, weighed, and had their stomach contents extracted and preserved in 80% ethanol (staghorn sculpin n=937, 92-329 mm TL; Dolly Varden n=448, 121-516 mm FL). Once all contents were removed from a stomach, they were weighed together to obtain a total blotted wet weight. Next, individual prey items were identified to the lowest taxonomic level possible using fish and invertebrate identification keys (McCafferty 1983, Kozloff et al. 1987, O'Clair and O'Clair 1998, Harvey et al. 2000, Mecklenburg et al. 2002), counted, measured, weighed, and assigned a condition code based on the extent of digestion observed (Beaudreau and Essington 2009, Alaska Fisheries Science Center 2015).

We used the presence or absence of otolith thermal marks to distinguish between hatchery and wild salmon (i.e. Volk et al. 1999). Like most large hatcheries in Alaska, Macaulay Salmon Hatchery marks 100% of the fish they release (Stopha, 2017). We extracted otoliths from chum salmon captured in beach seines and found in predator stomachs to determine origin. After removal, sagittal otoliths were cleaned before being mounted to a glass slide with clear resin. Mounted otoliths were then ground on abrasive discs to expose the primordia and any thermal marks diagnostic of hatchery origin (Courtney et al. 2000). Marks were evaluated using a compound microscope with the assistance and expertise of the Alaska Department of Fish &

Game Mark, Tag, and Age Laboratory (10107 Bentwood Drive, Juneau, AK, 99801). Macaulay Salmon Hatchery and other regional hatcheries mark 100% of the chum salmon they release, so fish without any otolith thermal mark were interpreted as wild born. Origin determination was done for all chum salmon identified in predator diets that had recoverable otoliths (n = 158). In beach seine catches, origin was determined for retained subsamples from early May to early June of 2016, and from early May to late May of 2017, the time periods when most predation on chum salmon occurred (n = 261; Appendix A). In April of 2017, no hatchery releases had occurred and all chum salmon in predator diets during the month were determined to be wild-born, so beach seine catches were assumed to be of wild-born.

Data analysis

Diet composition of predators

To assess the contribution of chum salmon to predator diets, we used the standard indices proportion by weight (W_i) and frequency of occurrence (O_i) (Chipps and Garvey 2007). W_i, calculated by dividing prey group weight by total prey weight, was used to provide information about the energetic contribution of prey groups to a predator's diet. O_i, the number of predator stomachs containing a prey item divided by the total number of sampled stomachs including those without contents, indicates what proportion of predators incorporated a specified prey group into their diet. Non-biological material, parasites, vegetation, and rocks found in stomachs were excluded from analyses.

Size- and origin-based patterns of predation

We quantified prey size spectra to assess size-based relationships (Scharf et al. 2000) between the focal predators and salmon prey. These diagrams relate predator body length to prey body length and indicate the range of prey lengths consumed by individuals across the sampled

size range (Pearre 1986). Quantile regression (R package 'quantreg', R Core Team 2017) was used to fit the upper (95th quantile) and lower (5th quantile) boundaries of prey length consumed as a function of predator length (Scharf et al. 1998). Boxplots were used to compare length frequency distributions of chum salmon released from hatchery net pens, caught in beach seines, and found in predator stomachs over each sampling year. As only a subsample of chum salmon was analyzed for origin, these plots do not distinguish hatchery- and wild born fish. When origin was known, one-way analyses of variance (ANOVA), followed by Tukey's Honestly Significant Difference (HSD) post-hoc tests, were used to evaluate differences in mean length among chum salmon caught in the beach seine, released from hatchery net pens, and found in stomachs. Shapes of size distributions were also compared among chum salmon groups using Kolmogorov-Smirnov (K-S) tests. These comparisons allowed us to infer potential size-selectivity by comparing the lengths of chum salmon consumed to the lengths of the chum salmon present at the sites.

Spatial and temporal patterns of predation

To visualize spatial and temporal patterns of predation on salmon, we plotted the mean standardized mass of chum salmon consumed per predator and mean (±SE) chum salmon catch-per-unit-effort from beach seines across sites for each sampling period. CPUE was calculated as the average juvenile chum salmon catch per set of both 15.2 m seines for each seine sampling day.

To characterize the temporal shift in potential availability of hatchery salmon to predators, we used logistic regression to determine the probability that chum salmon captured in beach seines or found in predator stomachs were of hatchery origin as a function of sampling date with the binary response variable being the origin, hatchery or natural, of juvenile chum

salmon in known samples. Due to low sample sizes, origin data for chum salmon from seines catches and predator stomachs were combined into a single analysis. Analyses were performed separately for each year because sampling was only conducted after hatchery releases had already occurred in 2016 due to permitting delays.

Factors explaining variation in predation of chum salmon

We used a multiple regression approach to identify the extent to which predation on juvenile chum salmon could be explained by the date, location of sampling, predator size, and the relative densities and origins of juvenile salmon. As most sampled predators did not incorporate salmon into their diets, the response variable—chum salmon in diets—is zero-inflated. To address this, we modeled the occurrence (presence/absence) and quantity (standardized mass) of salmon consumed in two stages, following the approach used by Beaudreau and Essington (2007) and detailed below. Regression analyses were performed separately for staghorn sculpin and Dolly Varden. Predators with empty stomachs, approximately 1% of individuals from each species, were excluded from analyses.

First, we estimated the probability of juvenile chum salmon occurrence in predator stomachs using multiple logistic regression, with the binary response variable being the presence or absence of chum salmon in a predator's stomach. The full model included the following predictors: year, day of year, site, predator length, and juvenile chum salmon CPUE. Site, rather than distance from the nearest hatchery net pen, was selected as a predictor because chum salmon from multiple release sites are known to mix at individual study sites (A. Zaleski, personal communication, 1 May 2018); site also accounts for differences that may have been caused by other variables that were not measured.

We then used multiple linear regression to model the quantity of salmon consumed when present. The response variable was the standardized mass of chum salmon, calculated as chum salmon prey weight divided by predator weight (minus stomach contents) raised to 0.75, the assumed allometric slope of consumption for teleosts (Essington et al. 2001), to control for the effects of predator size on consumption rate (i.e., consumption rates increase with body size). The full model included the same potential predictors as the logistic regression model plus one additional parameter for staghorn sculpin, the proportion of hatchery-born chum salmon present during a given seine sampling event. The proportion of hatchery salmon was not included as a factor in Dolly Varden models because relative densities of hatchery salmon were unavailable for the days when Dolly Varden were sampled using hook-and-line. Predator length was included to determine if quantity consumed was higher or lower than could be explained by expected size-based increases in consumption alone. Diagnostic probability plots generated from the full model showed nonlinearity, so a square root transformation of the response was selected for Dolly Varden and a log transformation for staghorn sculpin using the Box–Cox procedure (Weisberg 1985).

For both logistic and linear regression analyses, we used Akaike's information criteria, bias-corrected for small sample size (AICc), to identify the best explanatory model or set of models. Following convention, models with AICc values within 2 units of each other (ΔAICc $\leq$ 2) were considered to perform equivalently (Burnham and Anderson 2002). To identify predictors with the highest relative importance in explaining variation in occurrence or quantity of salmon in diets, we calculated Akaike parameter weights $w+(j)$, which scale from 0 to 1 and are interpreted as the weight of evidence in support of a given parameter's inclusion in the best model (Burnham and Anderson 2002). The Akaike parameter weight of parameter j is calculated

as the sum of model weights (relative likelihoods) across all models that included parameter *j* (Burnham and Anderson 2002).

Results

Contribution of chum salmon prey to predator diets

Across sites and years, juvenile salmon made up 6.5% of staghorn sculpin diets by weight; specifically, 4.5% of the diet consisted of chum salmon, 2.0% was coho salmon, and less than 0.1% was not identifiable to species level. Chum salmon occurred in 2.8% of staghorn sculpin stomachs sampled. Of 54 chum salmon identified in staghorn sculpin stomachs across sampling periods, otoliths were recovered and successfully evaluated for 47 individuals. 87.2% were found to be of hatchery-born. By weight, the remainder of staghorn sculpin diet was composed of other teleosts (52.3%), invertebrates (38.1%), and eggs or unidentifiable tissue (3.1%; Appendix Table B). The teleost contribution was dominated by Pacific sand lance (*Ammodytes hexapterus*; 14.5%) and Pacific herring (*Clupea pallasii*; 13.2%). Approximately 9.3% of fish prey were not identifiable to a taxonomic level below Teleostei. The invertebrate category was primarily composed of isopods (13.1%), annelid worms (8.3%), crabs (Pleocyemata; 6.5%), amphipods (3.0%), and unidentified crustaceans (3.7%). All other individual invertebrate prey groups made up 2% of the diet, or less, by weight.

For Dolly Varden, juvenile salmon made up 34.9% of the diet by weight, specifically 19.6% chum salmon, 15.0% coho salmon, and 0.3% unidentifiable salmon. Chum salmon occurred in 10.0% of Dolly Varden stomachs. Of 136 chum salmon identified in Dolly Varden stomachs, 111 were successfully screened for origin and 91.9% were found to be of hatchery-born. The remainder of Dolly Varden diets consisted of 39.5% teleost and 22.0% invertebrates

by weight (Appendix Table B). Prey fish were predominantly Pacific herring (22.3%) and Pacific sand lance (8.0%). Other relatively important fish prey groups included Stichaeidae (pricklebacks; 4.2%), Agonidae (poachers; 1.8%), and unknown teleosts (1.8%). The most prevalent invertebrate prey groups were amphipods (12.3%) and cumaceans (4.1%), which occurred frequently in Dolly Varden diets (in 63.6% and 57.6% of stomachs, respectively) and composed a high percent of the diet by number (Appendix Table B). While many other invertebrate prey groups were consumed, including insects, all were 2% by weight or less of the total diet.

Size- and origin-based patterns of predation

The prey size spectrum for staghorn sculpin was wedge-shaped, illustrating that as sculpin length increased, both longer fish prey and a wider size range of prey fish were consumed (Figure 2a). The estimated slopes of upper and lower bounds from the quantile regression were significant (95^{th} quantile: $\beta = 0.546$, $P < 0.001$; 5^{th} quantile: $\beta = 0.047$, $P < 0.001$); however, the relatively flat slope of the lower bound indicates that the minimum size of fish prey consumed did not change substantially over sampled size classes. Focusing on salmon prey, staghorn sculpin across the sampled size range incorporated chum salmon into their diets, and the lengths consumed were largely consistent across predator lengths, with an average (±SD) size of 51.9 mm SL (±6.9 mm).

The Dolly Varden prey size spectrum was also wedge-shaped (Figure 2b). The estimated slopes of upper and lower bounds from the quantile regression were significant (95^{th} quantile: $\beta = 0.209$, $P < 0.001$; 5^{th} quantile: $\beta = 0.024$, $P < 0.001$). When considering only salmon prey, Dolly Varden consumed a wider range of chum salmon lengths compared to staghorn sculpin, and salmon prey length generally increased with predator length (Figure 2b). Dolly Varden

across the sampled size range consumed chum salmon and the average (±SD) length of chum salmon prey was 48.5 mm SL (±12.1 mm).

When origin was known for all chum salmon sample groups (i.e., early May to early June of 2016 and early April to late May of 2017) they exhibited significant variability in length depending on origin and sampling group (ANOVA: $F = 187.2$, $DF = 4$, $P < 0.001$; Figure 3). Chum salmon from hatchery net pens at release (60.7 mm SL ±9.5 mm) and hatchery chum salmon captured in beach seines (60.1 mm SL ±8.3 mm) were not found to be significantly different in average length (HSD: $P = 0.931$) or distribution (K-S test: $D = 0.092$, $P = 0.126$). Hatchery chum salmon in beach seine catches were significantly longer than measurable hatchery chum salmon found in both predators' stomachs (50.7 mm SL ±10.1 mm; HSD: $P < 0.001$) and had significantly different length distributions (K-S test: $D = 0.418$, $P < 0.001$). Hatchery chum salmon in beach seine catches were significantly longer than wild born chum salmon in beach seine catches (39.9 mm SL ± 7.8 mm SD; HSD: $P < 0.001$) and had different distributions (K-S test: $D = 0.828$, $P < 0.001$). The mean lengths of wild born chum salmon in beach seine catches and predator stomachs (38.7 mm SL ±9.4 mm) were not significantly different (HSD: $P = 0.994$) but did show evidence of originating from different distributions (K-S test: $D = 0.407$, $P = 0.029$). Across all sampling periods, chum salmon of all origins (including unknown) found in staghorn sculpin stomachs (51.9 mm SL ± 6.9 mm) and Dolly Varden stomachs (48.5 mm SL ±12.1 mm) were shorter on average than chum salmon released from the hatchery (60.7 mm SL ±9.5 mm) or captured in beach seines (57.3 mm SL ±10.6).

Boxplots showing length frequency distributions of chum salmon released from hatchery net pens, caught in beach seines, and found in predator stomachs at each sampling period (Figures 4 and 5) show similar patterns to the size distribution data aggregated across sampling

periods. Specifically, predators consumed smaller chum salmon individuals compared to those in beach seine catches and hatchery net pens. The only exception was for Dolly Varden in late May of 2016, which consumed chum salmon prey of a larger average length (64.3 mm ± 7.3 mm SD) than chum salmon caught in the seine (62.4 mm ±8.9 mm) and released from the hatchery (63.2 mm ±9.3 mm).

Spatial and temporal patterns of predation

Qualitatively, temporal trends in the mean mass of chum salmon consumed mirrored trends in beach seine chum CPUE, which we use as a proxy for availability of chum salmon prey and followed similar relative trends across sites. In April, chum salmon catches and quantity in predator diets were low; on average, catches and consumption of chum salmon increased in early May, were highest in late May, declined in early June, and were low again in late June and early July (Figure 6). The contribution of chum salmon by weight to predator diets varied across sites; the W_i ranged from 1.1-2.6% for Cowee Creek, 0.6-0.1% for Eagle River, 12.4-16.6% for Mendenhall River, and 1.7-37.3% for Sheep Creek.

The probability that chum salmon in seine catches and stomachs were hatchery born increased dramatically after hatchery releases (Figure 7). In 2016, all sampling was conducted after hatchery releases and day of year was not a significant predictor of origin based on logistic regression ($z=-0.049$, $DF=1$, $P=0.961$), as the probability of being a hatchery fish was estimated to be uniformly high (~85%) from early May to early June. In 2017, hatchery chum salmon releases did not occur until after the early May sampling period, and day of year was a significant predictor of the probability that a chum salmon was of hatchery origin ($z=8.247$, $DF=1$, $P<0.001$, $\beta=0.349$). At Mendenhall River and Sheep Creek estuaries, the two sites where the numbers of salmon in predator stomachs were greatest, the proportions of hatchery chum

salmon in diets after hatchery release (86-95%) were similar to the proportions of hatchery chum salmon found concurrently in beach seine catches (85-100%).

Factors explaining variation in predation of chum salmon

For staghorn sculpin, the top logistic regression model (lowest AICc) predicting occurrence of chum salmon included the parameters site, day of year, predator length, and chum salmon CPUE; however, three other candidate models received equivalent support (Table 3). The best linear regression model for quantity of salmon prey included the predictors predator length and proportion of hatchery fish present at the site (Table 3). Two other models received equivalent support based on AICc and included the predictors salmon CPUE, predator length, and proportion of hatchery fish. Parameter weights $w+(j)$ calculated from all fitted models indicated that site and day of year were the most important factors ($w+(j) > 0.8$) explaining occurrence of chum salmon in staghorn sculpin stomachs, while chum salmon CPUE was moderately important ($w+(j) > 0.6$), and year and predator length were relatively unimportant ($w+(j) < 0.3$; Table 4). The proportion of hatchery chum salmon and predator length were relatively important ($w+(j) > 0.7$), salmon CPUE was moderately important ($w+(j) = 0.589$), and day of year, year, and site were relatively unimportant ($w+(j) < 0.2$) in explaining variation in the quantity of chum salmon in the diets (Table 4). The probability of consuming chum salmon was highest at the Mendenhall river and Cowee Creek sites, decreased with sampling date, and increased with salmon CPUE (Appendix Table C). The estimated quantity of chum salmon consumed decreased with predator length and increased with the proportion of hatchery chum salmon present and chum salmon CPUE (Appendix Table D).

For Dolly Varden, the best logistic regression model included site, year, day of year, and chum salmon CPUE as predictors of occurrence of chum salmon in diets; one other model,

which also included predator length, received equivalent support (Table 2). The best linear regression included only the predictor day of year, but there was equivalent support for the model including year and day of year, as well as the model including day of year and predator length (Table 3). Parameter weights $w+(j)$ indicated that site, day of year, and year were the most important factors ($w+(j) > 0.8$) explaining variation in occurrence of chum salmon in Dolly Varden stomachs, while chum salmon CPUE and predator length were unimportant ($w+(j) < 0.1$; Table 4). Day of year was important ($w+(j) > 0.9$) and all other predictors were relatively unimportant ($w+(j) < 0.4$) in explaining variation in standardized mass of chum salmon in the diets (Table 4). The probability of consuming chum salmon was highest at the Sheep Creek and Mendenhall River, higher in 2017 than 2016, and decreased with sampling date (Appendix Table C). The estimated quantity of chum salmon consumed increased with sampling date (Appendix Table D).

Discussion

Our results help illuminate a poorly known but widely believed critical life history bottleneck in Pacific salmon demography by quantifying the diets of two abundant nearshore predators, staghorn sculpin and Dolly Varden. Across two seasons we found that juvenile chum salmon were consistent components of their diets during the spring period of hatchery releases and outmigration of wild-born salmon. A majority of the chum salmon consumed were hatchery-born and most were smaller than chum salmon released from the hatchery or captured in beach seines. However, wild-born chum salmon in predator stomachs were not significantly longer or shorter than wild-born chum salmon caught in beach seines. Day of year, site, and chum salmon

CPUE were consistently important factors explaining variation in chum salmon occurrence and quantity in predator diets.

Size- and origin-based patterns of predation

The average length of chum salmon consumed was lower than the average length of chum salmon caught in seines and released by the hatchery. This result is consistent with research showing a preference for smaller prey by piscivorous fishes (Juanes 1994, Sogard 1997, Scharf et al. 2000), as well as studies of size selective mortality on juvenile salmon that found higher mortality rates among smaller individuals (Parker 1971, Healey 1982, Duffy and Beauchamp 2008). However, wild-born chum salmon in diets were not significantly different in length or distribution than wild-born chum salmon in beach seine catches. This may suggest different patterns of selectivity for wild-born fish, perhaps due to behavioral differences, but could also be an artifact of small sample sizes for wild-born fish in both diets and beach seine catches. Overall, our results indicate predators were selective for smaller than average fish, with the caveat that the assessment of chum salmon sizes potentially available to consumers was influenced by beach seine selectivity. We periodically observed the smaller size classes of chum salmon escaping through the mesh of our net which may have resulted in the underrepresentation of smaller size classes. Furthermore, the beach seines were not able to capture fish that had migrated further offshore but were still within the foraging range of the mobile consumers.

We rarely found the largest size classes of chum salmon caught in beach seines or released from the hatchery in predator diets, particularly in 2017. This is noteworthy because as a strategy to minimize early marine predation, Macaulay Salmon Hatchery holds and feeds some chum salmon in net pens for an extra 2-3 weeks to grow them to a larger size before release. Over the period of this study, 44% of hatchery chum salmon were released at or above a 4 g

average weight threshold, which corresponds to a length of approximately 66 mm SL, based on a length-weight regression that we developed from chum salmon sampled in hatchery net pens immediately before release (unpublished data). Hatchery chum salmon of the same length captured in beach seines post-release had an average weight of approximately 3 g. This difference in weight may be an artifact of the hatchery weighing their fish after feeding, thereby obtaining a higher weight compared to the released fish (B. Meredith, personal communication, 24 May 2018), or due to reduced condition of released fish resulting from the transition from net pen feeding to natural foraging (Reese et al. 2009, Sturdevant et al. 2012). In contrast, the average size of a wild-born chum salmon in our seine catches was just 0.93 grams, or 39.9 mm SL. The intent of enhanced growth in hatchery fish is to improve survival by increasing escape ability and minimizing the amount of time fish spend in nearshore habitats. Increased size at marine entry has been shown to improve salmon smolt survival in both hatchery and natural settings (Healey 1982, Hargreaves and Lebrasseur 1985, Willette et al. 2001). Our results appear to support the effectiveness of this strategy for reducing predation by staghorn sculpin and Dolly Varden, as 93% of measurable chum salmon prey were below the 66 mm average release size target. While increased size at release may help hatchery chum salmon avoid predation at marine entry, it is important to note the potential drawbacks including match/mismatch dynamics with predators or food resources later in their life history and earlier maturation leading smaller returning adults (McConnell et al. 2018) that are less desirable in fisheries (Morita et al. 2005).

Spatial and temporal predation patterns and factors affecting predator responses

Day of year was one of the most important predictors explaining chum salmon occurrence in predators' diets. This reflected the strong seasonality of juvenile chum salmon presence in estuaries due to outmigration and hatchery release timing. Site was of almost equal

importance to day of year in predicting occurrence of chum salmon prey in the diets of both predators. While we were not able to sample before releases in 2016, there were very low predator abundances and incorporation of chum salmon into diets prior to releases in 2017, suggesting that predators may not use salmon heavily early in the season.

Our hypothesis that the contribution of chum salmon to predator diets would be greatest at sites closest to hatchery release areas was not fully supported. The proportion of chum salmon in predator diets was variable but highest at Sheep Creek (nearest to hatchery release area) and Mendenhall River (third nearest) estuaries and relatively low at Eagle River and Cowee Creek estuaries (second and fourth nearest, respectively). Despite the proximity of Eagle River estuary to a hatchery release site, chum salmon are released near the south side of the river delta and may move offshore or southward, rather than northward along the delta where we sampled. Fine-scale migration routes of juvenile salmon out of the nearshore waters are unknown and likely variable among years. All sites showed similarly high proportions of hatchery chum salmon in the beach seines after multiple hatchery releases had occurred in May. This suggests that hatchery fish are widely distributed after release but aggregate more heavily in certain areas, which is supported by Macaulay Salmon Hatchery's unpublished data on juvenile chum salmon movement (A. Zaleski, personal communication, 1 May 2018). Variability in chum salmon CPUE in relation to distance from hatchery release site indicates that proximity alone may not be a useful indicator of hatchery impact. Factors such as bathymetry, currents, temperature, habitat, salmon density, and food availability have been shown to play role in where salmon aggregate during early marine residency (Orsi et al. 2000, Sturdevant et al. 2012).

While seasonal patterns of chum salmon CPUE and proportion of hatchery chum salmon in seines were similar across sites, the absolute CPUE differences among sites could be large.

Chum salmon CPUE was positively related to both occurrence and quantity of chum salmon in predator diets, but only a moderately important predictor for staghorn sculpin and of low importance for Dolly Varden. Sites with relatively low proportions of chum salmon in predator diets, Cowee Creek and Eagle River, averaged 6.6 chum salmon per beach seine set. Mendenhall River and Sheep Creek, which had higher proportions of chum salmon in the diets of both predators, averaged 36.5 chum salmon per set. This suggests a positive functional response, which is common as prey encounter rates impact probabilities of capture for piscivores (Juanes et al. 2008), suggesting that differences in chum salmon density, while not strongly reflected in the models due to high variability in daily catch averages, likely contributed to differences in predation observed among sites. The lower importance of CPUE for Dolly Varden may also reflect their mobile nature. Dolly Varden move daily and seasonally to optimize foraging (Armstrong 1970, Schutz and Northcote 1972). In contrast, staghorn sculpin exhibit more sedentary ambush tactics to capture prey (Mace 1983). Our CPUE measurements only reflect juvenile salmon densities in a small, intertidal area and may not be representative of densities further offshore or in adjacent habitats that active predators could access more easily.

Differences in predator preference for hatchery- and wild-born chum salmon is of interest to hatchery operators and salmon managers. Overall, more than 88% of chum salmon prey were of hatchery origin. This is similar to the proportion of chum salmon in beach seines that were determined to be of hatchery origin at times of peak chum salmon consumption (80-100%), which suggests that predators consumed chum salmon relative to their abundance in the environment (i.e., no preference based on origin alone). Hatchery- and wild-born salmon can occupy different habitats during nearshore residency (Reese et al. 2009, Sturdevant et al. 2012) and migrate into offshore habitats at different times (Orsi et al. 2004). Therefore, given the

limited geographic scope of our sampling, we were not able to assess preference quantitatively. It is also important to note that wild-born chum salmon have a higher expected smolt to adult survival rate than hatchery-born chum salmon (Kostow 2004), so the apparently limited predation on wild-born chum salmon may still have potentially significant implications for natural populations if predation rates are elevated compared to estuaries without any hatchery salmon input. All the sites evaluated for this study reached hatchery proportions of 85%, or higher, so we did not have a site with exclusively wild-born chum salmon to evaluate predation at as a baseline.

Predator length was a poor predictor of chum salmon occurrence in diets for both species, as chum salmon prey were consumed by nearly all sampled size classes of predators and did not appear to exceed the gape limitation of sampled predators. However, predator length was the second most important predictor of the quantity of salmon consumed by staghorn sculpin and the third most important for Dolly Varden. For both predators, the relationship between predator length and quantity was negative, indicating that small to intermediate size classes consumed more chum salmon relative to their body size. Staghorn sculpin generally transition from an invertebrate dominated diet at smaller sizes to incorporating more fish at larger sizes (Whitney et al. 2017), which is common among fishes, particularly for those with large gapes relative to body size (Mittelbach & Persson, 1998). The larger size classes of both predators tended to consume fish prey larger than juvenile chum salmon including Pacific sand lance, Pacific herring, and even juvenile coho salmon.

Conclusions

Staghorn sculpin and Dolly Varden, two abundant nearshore predators in Southeast Alaska estuaries, showed variable patterns of salmon consumption across sites and months. Most

salmon consumption coincided with relatively high salmon densities at sites in proximity to hatchery release areas. This suggests that hatchery releases provide an accessible food source that is used by nearshore consumers; however, hatchery subsidies to the nearshore food web are not new. The DIPAC Macaulay Salmon Hatchery has been producing and releasing juvenile salmon in the Juneau area since 1977. Ecological baselines from a system of exclusive natural production have likely shifted in ways that are unknown. Our understanding of the ecological effects of hatcheries would be greatly informed by research focused in times and places where hatchery production is just beginning, or where significant changes to hatchery release locations, numbers, or other release strategies are occurring, such as Eastern Prince William sound. Ultimately, determining whether nearshore predation by Dolly Varden and staghorn sculpin could have significant impact on salmon population dynamics and adult salmon returns requires more information about predator population sizes and their consumption rates, as well as other source of mortality. Estimated rates of salmon consumption by local predator populations could be used in population models for chum salmon that explicitly include predation as a source of natural mortality (e.g., Hollowed et al. 2000). Regardless, survival bottlenecks occurring later in chum salmon life history could render predation mortality at this stage less important. When developing any management strategy to improve salmon survival, it is imperative to identify and address the most intensive limiting life stages first.

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Figures

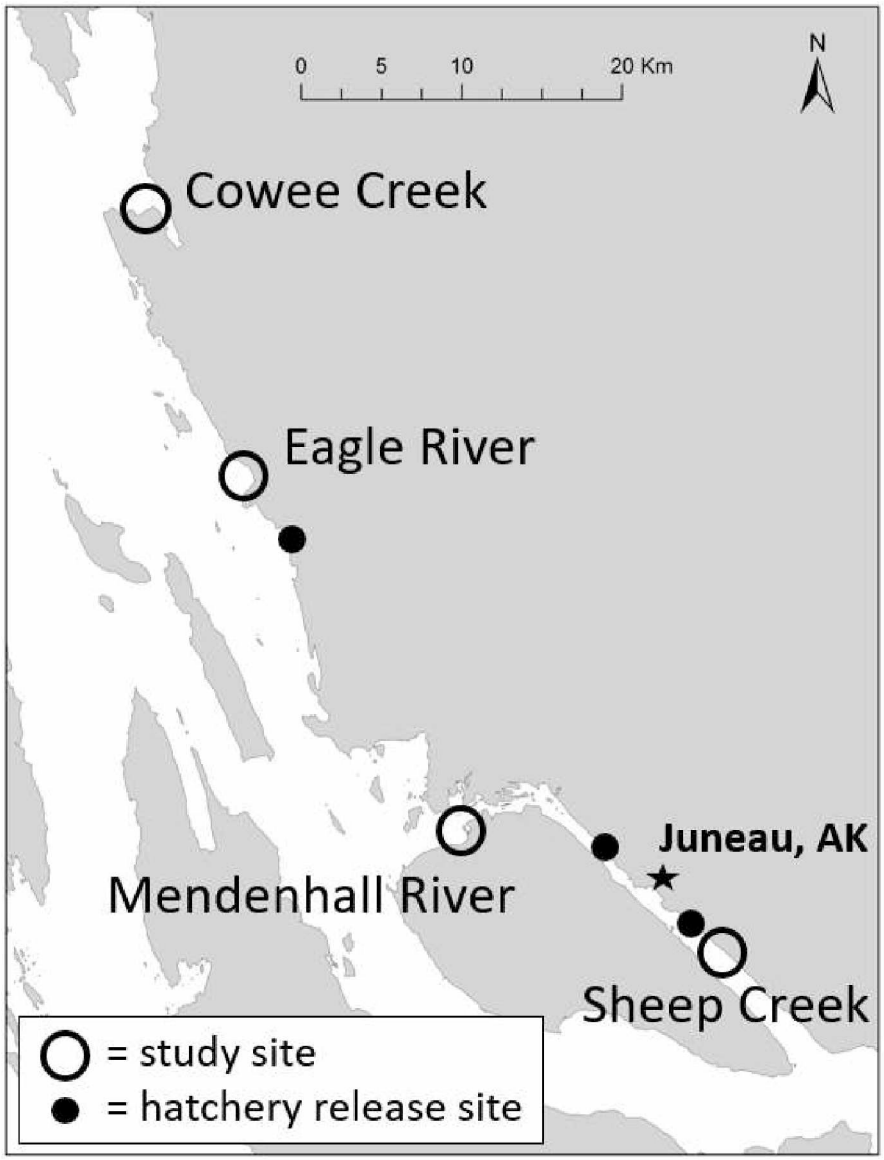

Figure 1.1 Map of study area indicating study sites (filled points) and hatchery release sites (hollow points).

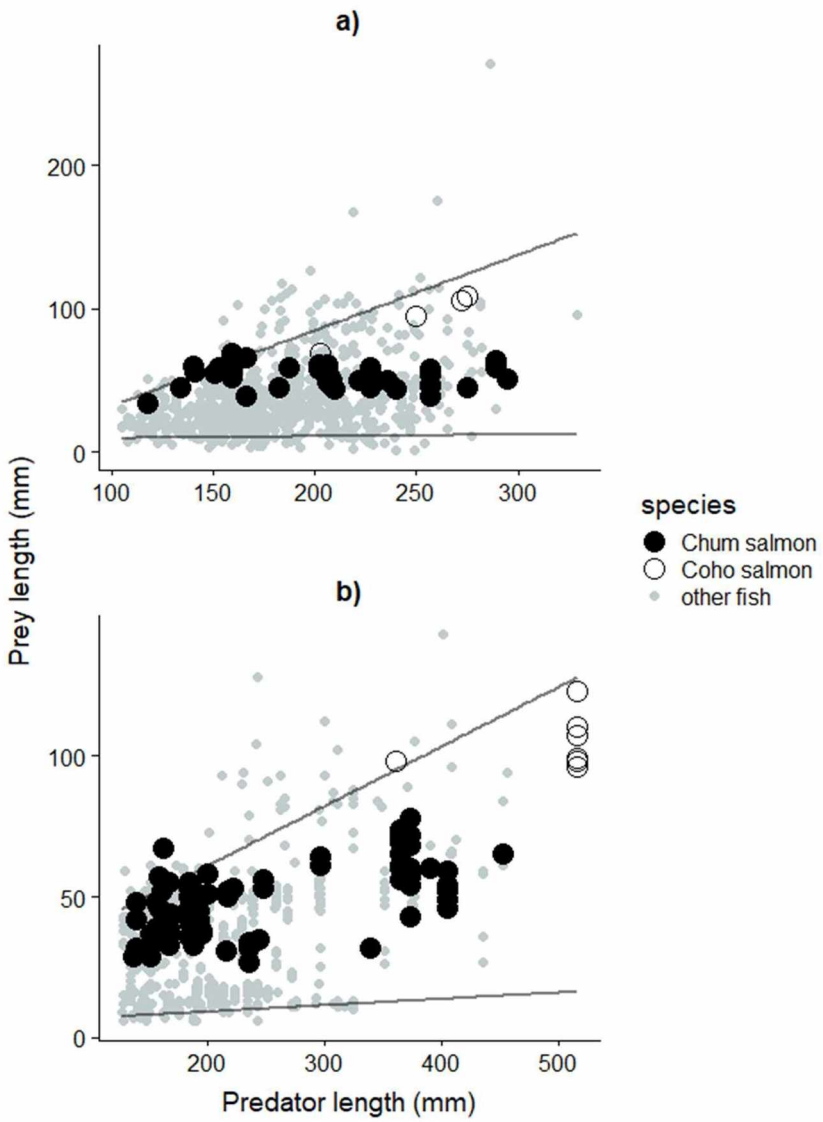

Figure 1.2 Prey size spectra for (a) staghorn sculpin and (b) Dolly Varden. Axis scales are different for each species.

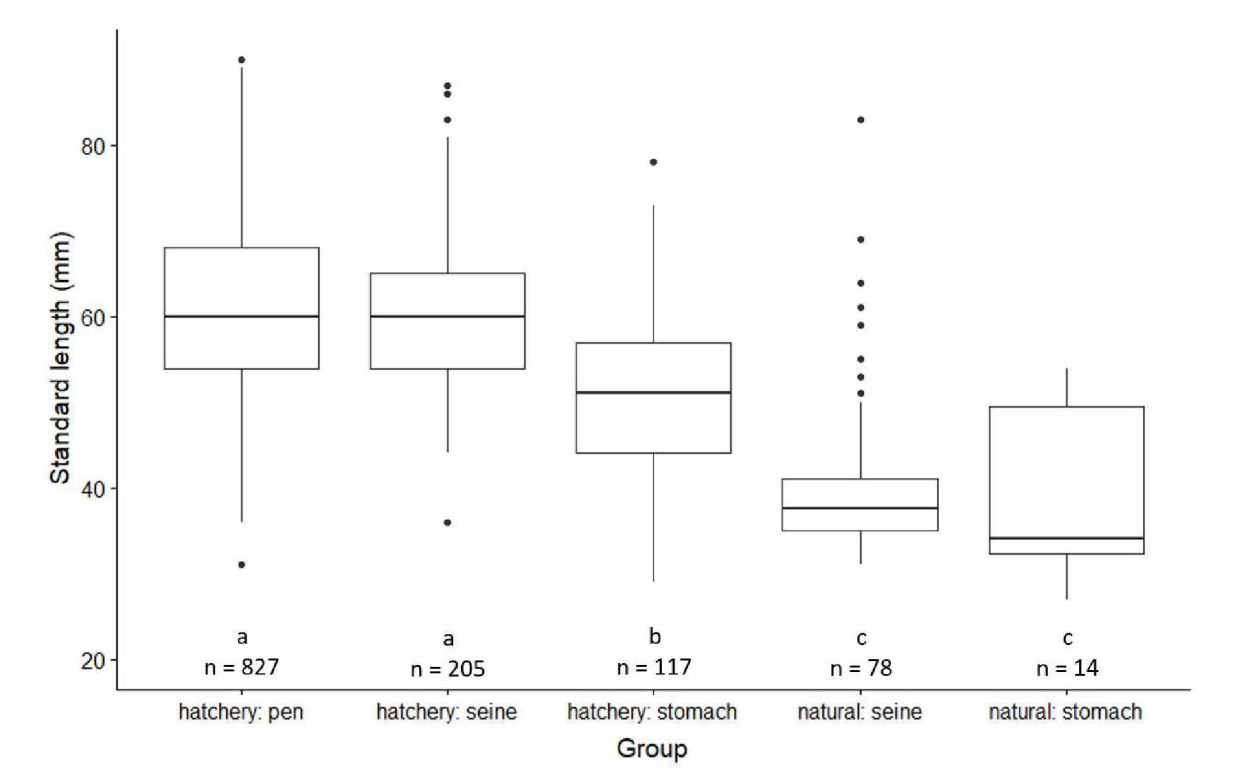

Figure 1.3 Length distributions of hatchery- and wild-born (natural) chum salmon from predator stomachs and beach seine catches. Differing letters indicate significant differences in mean length between groups, as determined by HSD.

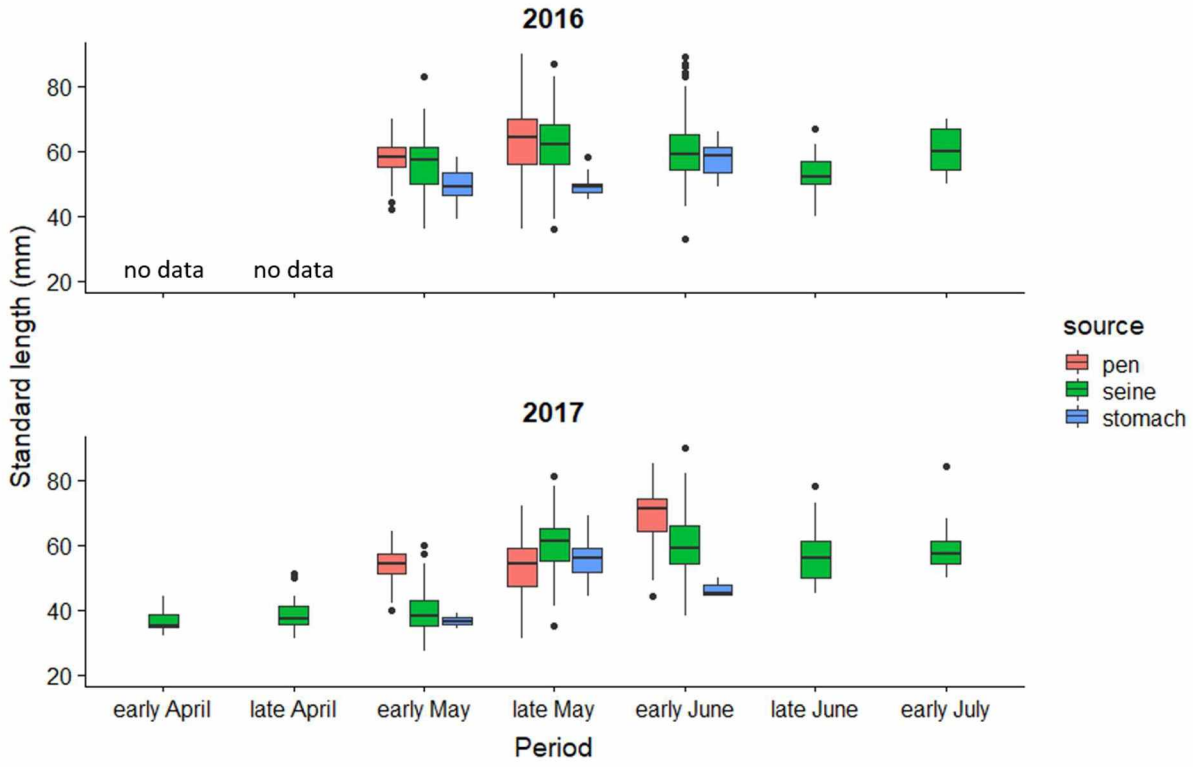

Figure 1.4 Length distributions of chum salmon captured in the beach seine, released from DIPAC hatchery net pens, and found in staghorn sculpin stomachs over time. Chum salmon from seine catches and predator stomachs include both hatchery and wild-born individuals, while net pen fish are exclusively hatchery origin.

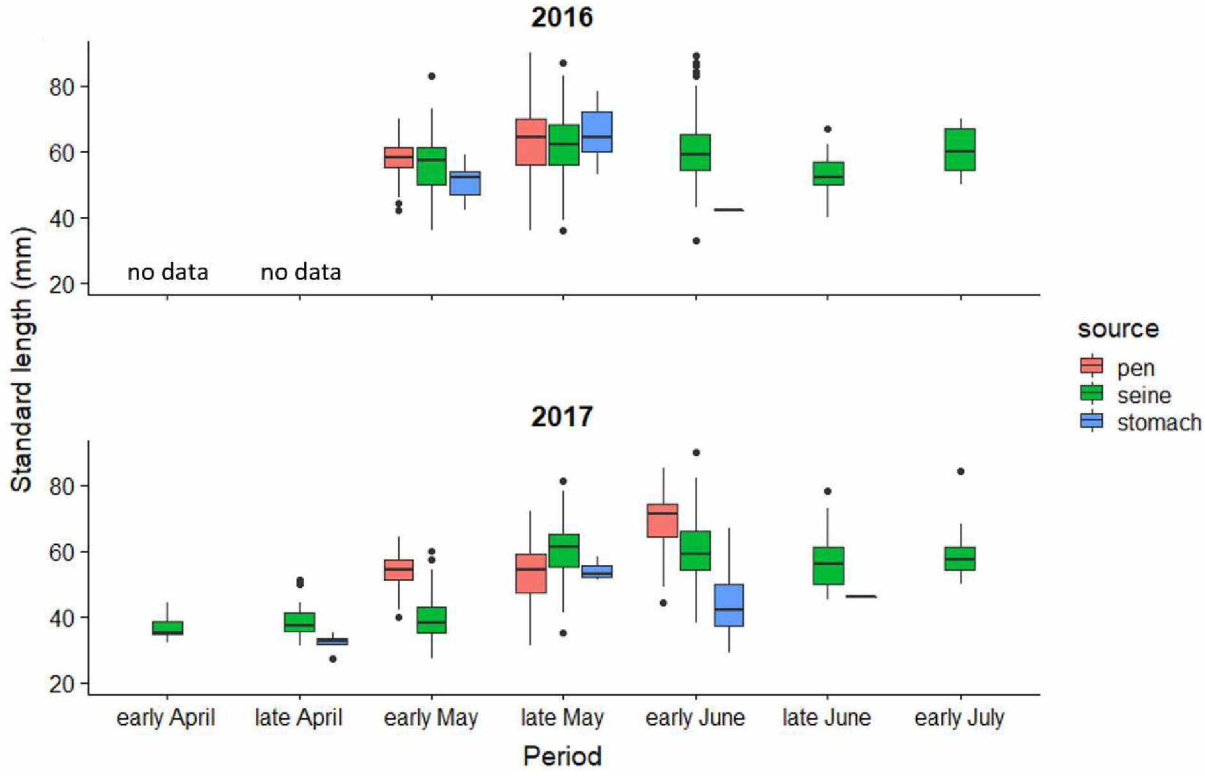

Figure 1.5 Length of chum salmon captured in the beach seine, released from DIPAC hatchery net pens, and found in Dolly Varden stomachs over time. Chum salmon from seine catches and predator stomachs include both hatchery and wild-born individuals, while net pen fish are exclusively hatchery origin.

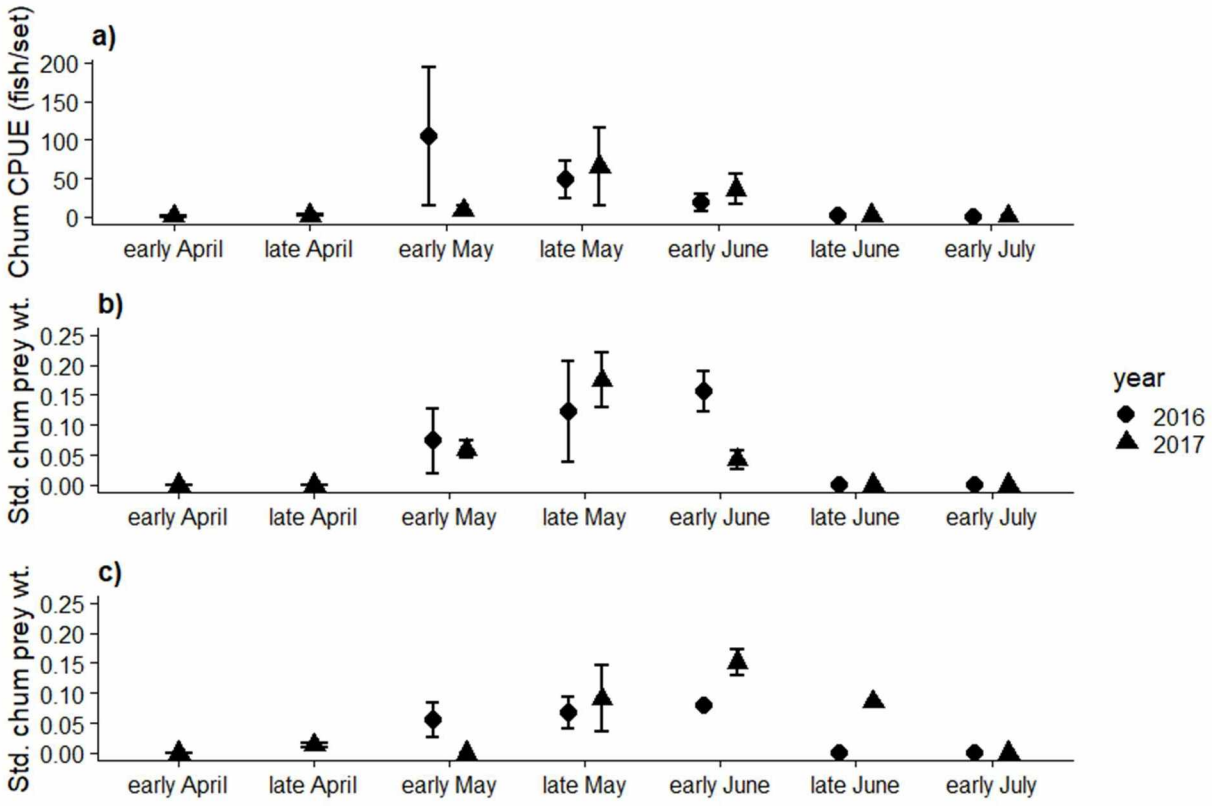

Figure 1.6 (a) Average chum salmon beach seine CPUE, and the average standardized mass of chum salmon in diets with chum salmon present for (b) staghorn sculpin and (c) Dolly Varden across sites and sampling periods, ± standard error.

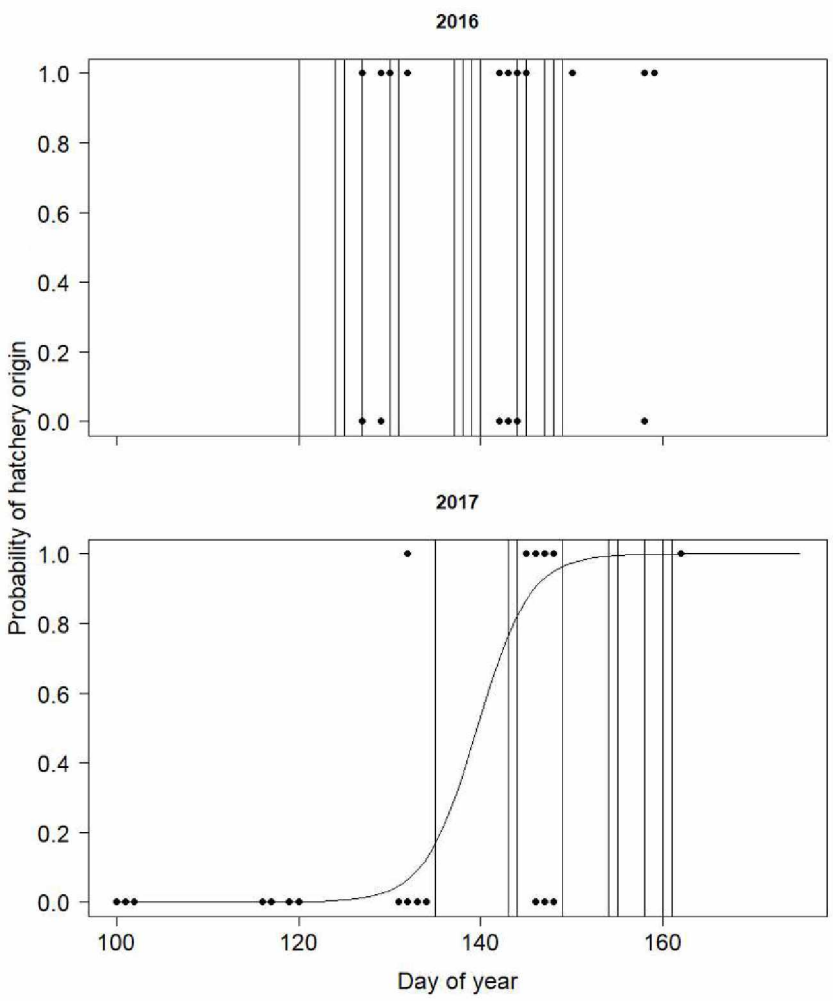

Figure 1.7 The occurrence of hatchery chum salmon, either caught in seines or found in diets, over time. Vertical lines indicate days that hatchery releases occurred. Day of year was not found to be significant in 2016 (n = 195), when the proportion of hatchery chum salmon in diets and seine catches averaged >85% the entire sampling season. For 2017, the curve is a fitted logistic regression estimating the probability of hatchery chum salmon occurrence over time (n = 281).

Tables

Table 1.1 Sampling periods with the number of seine sets conducted at each site and whether or not hook and line sampling occurred (Y/N). Only Dolly Varden were captured during hook & line sampling. ER = Eagle River, CC = Cowee Creek, MR = Mendenhall River, SC = Sheep Creek

		early April				late April				early May				late May				early June				late June				early July			
		ER	CC	MR	SC	ER	CC	MR	SC	ER	CC	MR	SC	ER	CC	MR	SC	ER	CC	MR	SC	ER	CC	MR	SC	ER	CC	MR	SC
2016	Seine sets									6	6	6	4	6	6	5	6	6	6	6	7	6	6	5	7	6	5	6	6
	Hook & line									N	Y	Y	Y	Y	Y	Y	Y	N	N	Y	N	Y	N	N	Y	N	N	N	N
2017	Seine sets	7	7	7	6	7	7	7	6	7	7	7	7	7	7	7	7	7	7	7	7	7	6	7	7	7	7	7	8
	Hook & line	N	N	N	N	N	N	N	N	N	N	N	Y	N	N	Y	N	N	Y	N	Y	N	N	N	Y	N	N	N	Y

Table 1.2 Model summaries for logistic regression on occurrence (presence/absence) of chum salmon in (a) Pacific staghorn sculpin stomachs (n=928), and (b) Dolly Varden stomachs (n=442). In total, 32 regression models for staghorn sculpin and 32 for Dolly Varden were evaluated that represented all combinations of predictors for each species. Predictors included site (factor), day of year, chum CPUE, year (factor), and predator length. K indicates the total number of parameters estimated, AICc is Akaike's information criteria, bias-corrected for small sample size, ΔAICc is a model's AICc with the lowest AICc of the model set subtracted from it, and w_i is the model Akaike weight.

Model #	Model Parameters	K	AICc	ΔAICc	w_i	Evidence ratio
(a) Pacific staghorn sculpin						
1	site + day of year + chum CPUE + predator length	8	190.4	0.0	0.291	1
2	site + day of year + chum CPUE	7	191.2	0.8	0.199	1
3	site + year + day of year + chum CPUE + predator length	9	191.9	1.4	0.142	2
4	site + year + day of year + chum CPUE	8	192.2	1.8	0.118	2
5	day of year + chum CPUE	4	193.6	3.2	0.058	5
6	day of year + chum CPUE + predator length	5	194.2	3.8	0.043	7
7	Null	2	239.2	48.8	<0.001	>100
(b) Dolly Varden						
1	site + year + day of year + chum CPUE	8	128.2	0.0	0.638	1
2	site + year + day of year + chum CPUE + predator length	9	130.3	2.0	0.232	3
3	site + day of year + chum CPUE	7	132.2	4.0	0.088	7
4	site + day of year + chum CPUE + predator length	8	134.1	5.9	0.033	19
5	site + year + chum CPUE + predator length	8	138.7	10.5	0.003	189
6	year + day of year + chum CPUE	5	139.6	11.3	0.002	291
7	Null	2	270.5	142.2	<0.001	>100

Table 1.3 Model summaries for linear regression on the standardized mass of chum salmon prey in (a) Pacific staghorn sculpin stomachs (n=26), and (b) Dolly Varden stomachs (n=40). 64 models were evaluated for staghorn sculpin with all combinations of the following predictors: site (factor), day of year, chum CPUE, year (factor), predator length, and proportion of hatchery chum present in seine catches (hatchery prop.). 32 models were evaluated for Dolly Varden with all combinations of the following predictors: site (factor), day of year, chum CPUE, year (factor), and predator length. K indicates the total number of parameters estimated, AICc is Akaike's information criteria, bias-corrected for small sample size, ΔAICc is a model's AICc with the lowest AICc of the model set subtracted from it, and w_i is the model Akaike weight.

Model #	Model Parameters	K	AICc	ΔAICc	w_i	Evidence ratio
(a) Pacific staghorn sculpin						
1	predator length + hatchery prop.	4	54.2	0.0	0.312	1
2	chum CPUE + predator length + hatchery prop.	5	54.8	0.5	0.239	1
3	chum CPUE + hatchery prop.	4	55.2	1.0	0.189	2
4	year + predator length + hatchery prop.	5	57.9	3.7	0.049	6
5	day of year + predator length + hatchery prop.	5	58.1	3.8	0.046	7
6	day of year + chum CPUE + predator length + hatchery prop.	6	58.5	4.3	0.036	9
7	Null	2	78.1	23.9	<0.001	>100
(b) Dolly Varden						
1	day of year	3	-55.5	0.0	0.486	1
2	year + day of year	4	-53.9	1.6	0.222	2
3	day of year + predator length	4	-53.5	2.0	0.181	3
4	year + day of year + predator length	5	-51.3	4.2	0.060	8
5	site + day of year	6	-47.7	7.7	0.010	48
6	site + predator length	6	-47.7	7.7	0.010	48
7	Null	2	-40.3	15.2	<0.001	>100

Table 1.4 Akaike parameter weights (W+(j)) for logistic regression on the occurrence (presence/absence) of chum salmon in predator stomachs and linear regression on the standardized mass of chum salmon prey in predator stomachs.

Parameter	**W+(j)**
Logistic regression – Pacific staghorn sculpin	
day of year	0.998
site	0.836
chum CPUE	0.654
year	0.345
predator length	0.075
Linear regression – Pacific staghorn sculpin	
hatchery prop.	0.928
predator length	0.717
chum CPUE	0.551
day of year	0.127
year	0.126
site	0.007
Logistic regression – Dolly Varden	
site	0.996
day of year	0.994
year	0.878
chum CPUE	0.130
predator length	0.001
Linear regression – Dolly Varden	
day of year	0.974
year	0.301
predator length	0.261
site	0.044
chum CPUE	0.005

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Chapter 2: Parameterization and application of a field-based consumption model for Pacific staghorn sculpin (*Leptocottus armatus*), a ubiquitous estuarine predator of the northeastern Pacific Ocean[2]

Abstract

Mortality in nearshore areas is widely thought to be a demographic bottleneck for Pacific salmon populations, though the agents of mortality are rarely known. Here we explore the potential role of the Pacific staghorn sculpin (*Leptocottus armatus*), a generalist consumer, highly abundant in estuaries from Alaska to California as a consumer on salmonids and other prey. To translate diet data into daily consumption rates, we determined staghorn sculpin gastric evacuation rates through controlled experiments and implemented a field-based consumption model. Feeding trials indicated 72 hours are needed for a staghorn sculpin to reach >99% gastric evacuation at 7.7 degrees C, which is representative of spring and early summer water temperatures in Southeast Alaska. A sigmoid function best described gastric evacuation over time and allowed us to determine the relationship between visual prey condition and time since ingestion required to implement this field-based technique. Field-based model estimates of undigested chum salmon prey weight were consistent with observed data and corroborated with values determined from a known length-weight relationship. Estimated daily consumption of juvenile chum salmon by staghorn sculpin ranged from 0 to 5.51 g/day, with an average rate of 0.04 g/day. Consumption rates of all prey items ranged from 0 to 35.01 g/day, with an average rate of 1.65 g/day. Mass-specific consumption rates indicated that monthly patterns of juvenile chum salmon consumption mirrored prey availability. We found slower gastric evacuation than

[2] Duncan, D. H., Beaudreau, A.H., Tullis-Joyce, P. (2018). Parameterization and application of a field-based consumption model for Pacific staghorn sculpin (*Leptocottus armatus*), a ubiquitous estuarine predator of the northeastern Pacific Ocean. Manuscript in preparation for submission to the Journal of Fish Biology.

previously determined for smaller staghorn sculpin in warmer waters. Staghorn population sizes are not known, but preliminary calculations suggest that very large, and likely implausibly so, populations would be required to consume even 1% of local hatchery chum salmon production.

Introduction

Knowledge of fish consumption rates allows for a more thorough understanding of ecological relationships and energy flow through food webs (Hansen et al. 1993). Consumption rates can be used to estimate the food requirements of predators, and conversely, their potential impact on prey populations (Beauchamp et al. 2007). This information can be incorporated into stock assessments or multispecies population models to provide improved estimates of natural mortality and understanding of ecosystem dynamics (Hollowed et al. 2000). Models that incorporate information about fish consumption rates, from large scale ecosystem modeling (Coll et al. 2007) to smaller scale food web studies (Baldwin et al. 2011), provide valuable information about how environmental or anthropogenic disturbances are likely to alter current ecosystem function (Holsman & Aydin 2015). Determining consumption rates for a broader range of fish species can improve the accuracy of future studies that use these tools by reducing the need to generalize parameters across species.

Fish consumption rates can be determined with multiple methods, each with unique data requirements and assumptions. Two common approaches for estimating consumption are bioenergetics models (Kitchell et al. 1977) and empirical observation (field-based methods; Bajkov 1935, Elliott & Persson 1978). Bioenergetics models work on a mass-balance principle where energy used by an organism must equal energy consumed (Ney 1993). This is a theoretically sound method that works well on cold-blooded organisms, but requires detailed

information about metabolism and other sources of energy use or loss (Hartman & Kitchell 2008). Determining values for these parameters require laboratory experiments with sensitive instrumentation (Hartman & Kitchell 2008, Ney 1993), which can present challenges due to cost or difficulty with animal husbandry. Although there are multiple field-based modeling frameworks for determining consumption, most have fewer data requirements than bioenergetics models and their parameters can be derived from in situ observation of fish stomach contents and measurement of gastric evacuation rate (Beaudreau & Essington 2009, Worischka & Mehner 1998). This allows for consumption estimates to be more easily obtained for species that do not have existing mass- and temperature-dependent respiration functions parameterized for bioenergetics models or resources to generate them. Corroboration of multiple independent models to derive consumption rates for a species of interest may ultimately be the most robust approach, as it generates a plausible range of consumption rates for fish feeding in the wild under variable conditions (Beaudreau & Essington 2009, Holsman & Aydin 2015, Worischka & Mehner 1998).

In this study, we parameterized and corroborated a field-based consumption model for an abundant consumer in coastal habitats of the North Pacific Ocean, the Pacific staghorn sculpin (*Leptocottus armatus*; hereafter referred to as staghorn sculpin). Staghorn sculpins are generalist consumers found in nearshore marine and estuarine habitats along the west coast of North America, from California to Alaska (Mecklenburg et al. 2002). In neritic areas, they can be one of the most commonly encountered marine sculpin species (Morris 1960, Whitney et al. 2017); for example, in Southeast Alaska estuaries, staghorn sculpin were the most commonly captured fish species, representing nearly 35% of all fish caught from 2013 to 2018 (Beaudreau, Duncan, & Whitney; unpublished data). Despite their ubiquity, little is known about their life history and

ecology. It is believed that staghorn sculpin spawn in intermediate salinity waters during the winter and move seasonally among nearshore habitats including the lower intertidal reaches of rivers, with larger mature individuals tending to occupy marine waters further offshore for much of the year (Tasto 1975). As they can represent a substantial biomass in nearshore habitats, they likely play an underappreciated role in energy transfer through these habitats over a broad latitudinal gradient.

While staghorn sculpins are not commercially or recreationally exploited, their prevalence in estuaries that serve as nursery habitats for species important to fisheries have raised questions about the possible impact of their predation (Armstrong 1991, Mace 1983, Duncan & Beaudreau in prep.). Diet studies have confirmed that staghorn sculpin consume species such as juvenile salmon (*Oncorhynchus* spp.) (Duncan 2018; Mace 1983; Whitney et al. 2017) and Dungeness crab (*Metacarcinus magister*) (Armstrong 1991). These studies provide information about the composition of staghorn sculpin diets but, except for Mace (1983), none have estimated consumption rates to determine cumulative impact. Mace (1983) determined gastric evacuation rates for small size classes of staghorn sculpin (50-100mm) that had been documented feeding and rearing in freshwater. The sizes of staghorn sculpin that have been found consume juvenile salmon in estuary habitats are substantially larger (118-295 mm) and subject to different environmental conditions that likely alter their gastric evacuation rate (Whitney et al. 2017, Duncan & Beaudreau in prep.).

In Southeast Alaska, chum salmon (*O. keta*) are vital to regional salmon fisheries and are supplemented by a fisheries enhancement program that releases nearly 600 million juveniles into the nearshore marine environment annually. Early marine mortality driven by predation has been found to be as high as 85% for chum salmon (Bax 1983, Healey 1982) and may be one factor

driving variability in adult returns (Beamish & Mahnken 2001). As staghorn sculpins overlap in space and time with juvenile salmon during this high mortality period, they are a good candidate to evaluate potential predation impact. An important step towards evaluating the component of juvenile chum salmon mortality contributed by staghorn sculpin predation in estuary rearing habitats is the development of consumption models that derive estimates of daily ration from field and experimental data. Therefore, the objectives of our study were to: 1) experimentally determine gastric evacuation rates of staghorn sculpin at spring and early summer water temperatures and use the experimental results to parameterize a field-based consumption model, 2) evaluate the field-based model estimates with a regression-based approach to back-calculate undigested prey weight, and 3) use the model to estimate seasonal consumption rates of salmon smolts by staghorn sculpin near Juneau, Alaska, USA. (Duncan & Beaudreau in prep). The model we developed can be applied to staghorn sculpins throughout their range, with appropriate temperature correction, and may be generalizable to other small sculpin species that are ubiquitous consumers in the North Pacific Ocean. This provides a useful tool to researchers seeking to estimate the predatory role of abundant sculpins in coastal ecosystems and how they may use juvenile salmon or other seasonally pulsed subsides.

Methods

Field sampling and stomach content analysis

To determine diet composition, staghorn sculpins (N = 937, 92-329 mm total length) were collected with beach seines near Juneau, Alaska, in 2016 and 2017 (Duncan 2018). In the laboratory, stomach contents were identified, weighed, and measured as described in Duncan (2018). Each prey item was also designated with a prey condition code (PC) describing the

visually estimated proportion of prey remaining (Beaudreau & Essington 2009, Alaska Fisheries Science Center 2015). Each PC value, from PC_1 to PC_6, represents a range of values for the estimated proportion remaining (i.e., PC_6: 1; PC_5: 0.75 to < 1; PC_4: 0.50 to < 0.75; PC_3: 0.05 to < 0.50; PC_2: < 0.05; PC_1: empty) that can be determined visually with reasonable accuracy (Beaudreau & Essington 2009).

Field-based consumption model parameterization

To estimate consumption by staghorn sculpins, we used the field-based consumption model developed by Beaudreau and Essington (2009). This technique is well suited to opportunistic consumers that do not continuously feed (e.g., ambush predators), as there are no *a priori* assumptions about feeding periodicity or gastric evacuation functional form (Beaudreau & Essington 2009, Holsman & Aydin 2015). According to this model, daily consumption was estimated by:

$$C_d = \frac{\sum_{n}^{n_{tot}} W_{i_n}}{T} \times 24$$

where C_d is daily consumption in grams calculated by the initial (undigested) weight W_i of each individual prey item n summed over all prey items found the stomach n_{tot}. T is the maximum time a prey item could have been in the stomach as determined from gastric evacuation rate experiments. W_i is determined by:

$$W_i = \int_0^T \frac{W_f}{P_t} \cdot \Pr\{t \mid PC\}$$

where W_f is the final (observed) weight of partially digested prey in the stomach from field-based sampling, P_t is the proportion of prey remaining at time t, and $\Pr\{t|PC\}$ is the probability of time t given the observed PC code. P_t and $\Pr\{t|PC\}$ were determined from gastric evacuation rate experiments.

Feeding trials to determine gastric evacuation rate

The primary factors affecting gastric evacuation rate in fishes are predator size, prey size and type, and temperature (Bromley 1994). To the extent possible, we controlled for these factors and established experimental conditions that were typical of staghorn sculpins feeding in estuaries during the period of juvenile chum salmon outmigration (April-early July). As detailed below, we selected staghorn sculpin sizes representative of those collected in estuaries that were capable of consuming juvenile salmon (Whitney et al. 2017), we provided a meal size similar to the observed mean relative prey weight in staghorn sculpin stomachs and conducted experiments in similar thermal conditions to those measured at captures sites in 2017.

Staghorn sculpins (N=32, 144-256 mm TL, 200 mm average TL) were captured with beach seines at sites along Lynn Canal and Gastineau Channel, near Juneau, Alaska. Fish used in gastric evacuation trials were transported in aerated containers to the University of Alaska Fairbanks' Juneau Fisheries Center and held in a flow-through experimental seawater system that draws water from Lynn Canal. Each fish was placed in individual 0.6 m x 0.9 m enclosures with gravel substrate and acclimated for at least 120 hours to laboratory conditions. Prior to conducting experiments, fish were weighed, measured, and held unfed for an average of 11 days to allow for the evacuation of residual stomach contents. Fish were randomly assigned a 2, 4, 8, 12, 18, 24, 36, 48, 60, or 72-hour digestion interval and fed a ration consisting of a whole, previously frozen juvenile salmon provided by the Douglas Island Pink and Chum Inc. hatchery, weighing approximately 3% of predator body weight. Ration weight was based on the average proportion of stomach content weight to predator weight measured from staghorn sculpin diet data (Beaudreau & Essington 2009; Duncan 2018). A minimum of 3 trials per time interval were

conducted. At the end of a digestion interval, the fish was immediately euthanized with an overdose of MS-222 and dissected to remove the stomach contents. The digested ration was assigned a prey condition code (PC) corresponding to the visually estimated proportion remaining and weighed to determine the actual proportion remaining. Aquarium temperatures were measured at the beginning, middle, and end of each experiment and averaged 7.7 °C (± 0.2 SD). Experimental thermal conditions were similar to those at the sites where staghorn sculpins were collected, based on temperature loggers deployed at four field sites at depths of approximately 6 m. Mean hourly water temperature was 8.3 °C (± 1.6 SD) across sites from early May to early July.

Determining the function describing gastric evacuation

To verify the efficacy of our controls, we used multiple linear regression to determine whether staghorn sculpin length, meal size, temperature, and pre-feeding fast duration had a significant relationship with the proportion of the ration remaining. Next, we modeled the temperature-dependent gastric evacuation function (i.e., proportion of initial meal remaining over time) using least-squares linear and nonlinear regression. Eight models were fit to the data: linear, square root, exponential, power exponential, logistic, logistic restricted, Gompertz, and sigmoidal (Beaudreau & Essington 2009). Akaike's information criterion corrected for small sample size (AICc) was used to identify the best model based on likelihood with a penalty for complexity (Burnham & Anderson 2002). Following convention, models with AICc values within 2 units of each other ($\Delta AICc \leq 2$) were considered to perform equivalently and models within 4 units of each other ($\Delta AICc \leq 4$) were considered to perform similarly.

Determining probability of time since ingestion to calculate W_i

The field-based model developed by Beaudreau and Essington (2009) back-calculates the initial weight of prey consumed by relating the estimated proportion of prey remaining in the stomach to the time it would need to spend in the stomach to reach that stage of digestion. The feeding experiments were used to determine the relationship between time in the stomach and estimated proportion of prey remaining (PC). Once the relationship is known, it can be applied to prey items where only PC is known (i.e., field-sampled stomach contents). Following Beaudreau and Essington (2009), the marginal probability of PC given time was determined using logistic regression on the presence/absence of a given PC across time as:

$$\Pr\{PC|t\} = \frac{\exp(\beta_0 + \beta_1 t)}{1 + \exp(\beta_0 + \beta_1 t)}$$

The probability of the first state of digestion reached, PC_5, was estimated by fitting a logistic model to the experimental data, where the binary response was a 1 if a prey item was assessed as a PC5 at a given time and a 0 if it was assessed as any other PC. Subsequent prey conditions were calculated sequentially:

$$Pr\{PC_4|t\} = Pr\{(PC_5 \cup PC_4)|t\} - \Pr\{PC_5|t\}$$

$$Pr\{PC_3|t\} = Pr\{(PC_5 \cup PC_4 \cup PC_3)|t\} - \Pr\{PC_5|t\} - \Pr\{PC_4|t\}$$

$$Pr\{PC_2|t\} = Pr\{(PC_5 \cup PC_4 \cup PC_3 \cup PC_2)|t\} - \Pr\{PC_5|t\} - \Pr\{PC_4|t\} - \Pr\{PC_3|t\}$$

PC6, which represents no digestion (i.e., prey had just been consumed), was never observed in diet data or digestion experiments and assumed to only occur at t=0.

The probability of time given PC was calculated using Bayes' theorem:

$$\Pr\{t|PC\} = \frac{\Pr\{PC|t\} \times \Pr\{t\}}{\Pr\{PC\}}$$

where Pr{PC|t} was determined as described above, Pr{t} was assumed to be uniform based on no observed feeding periodicity by staghorn sculpins (Beaudreau & Essington 2009), and

$\Pr\{PC\}$ was the sum of $\Pr\{PC|t\}$ across time intervals from 0 to T hours. T was set to 84 hours, the observed time until 99% evacuation.

Model application and corroboration

Per-capita consumption ($g \cdot d^{-1}$ per individual sculpin) and mass-specific daily consumption ($g \cdot g^{-1} \cdot d^{-1}$) were calculated using the field-based model. To evaluate monthly patterns while controlling for variation in sample size and predator size, we grouped predator stomach content samples into two-week periods and mass-specific consumption ($g \cdot g^{-1} \cdot d^{-1}$) was averaged. For each stomach examined, W_f and PC were determined for each prey item individually. Consumption rates of chum salmon and all other prey were calculated for each sampling period to assess monthly variation in consumption. To corroborate the field-based model, we compared W_i estimates for chum salmon prey to back-calculated weights of chum salmon prey with measurable lengths as determined from a chum salmon length-weight relationship derived from data on chum salmon caught in the beach seines. The correlation between estimators was evaluated with Pearson's correlation coefficient and differences were visualized with linear regression. Chum salmon prey too digested to determine standard length were excluded from the comparison. The number of staghorn sculpins required to consume a given number of juvenile chum salmon was estimated by first multiplying the mean daily consumption of chum salmon (in number of individuals assuming a 2 g mean weight) by the approximate period of chum salmon availability (90 days) to obtain the mean individual seasonal consumption. Then, the number of chum salmon to be consumed was divided by the mean individual seasonal consumption to determine how many staghorn sculpins would be required to consume that quantity.

Results

Consumption model parameterization

Time since ingestion was the only significant predictor of proportion of the meal remaining based on the multiple linear regression (t-test: t = 28.62, DF = 26, P < 0.001). Average experimental water temperature (t = 1.47, P = 0.238), staghorn sculpin length (mm) (t = 0.63, P = 0.536), ration size as a proportion of staghorn sculpin weight (t = 1.80, P = 0.083), and pre-trial fast duration (t = 0.37, P = 0.371) were not found to have a significant relationship with the proportion of ration remaining.

A sigmoid function best fit the observed gastric evacuation of staghorn sculpins (AICc = -164.4, Table 1, Figure 1). The power exponential function had equivalent support with an AIC of -162.8, but all other models did not perform as well. The sigmoid model ($\beta_0 = 0.033$, $\beta_1 = 0.746$) was selected for use in W_i estimation due to highest weight of evidence, ability to more easily constrain the intercept at 1, and the biological plausibility of the S-shaped curve representing an initial lag time as digestive processes increase from resting, peak, and slow as the stomach begins to empty (Persson 1986). The sigmoid function could not be solved for complete gastric evacuation, and time to 95% digestion was calculated as ~121 hours. However, >99% gastric evacuation was observed in all three of the longest duration (72 hour) feeding trials, so T was set conservatively at 84 hours.

We determined the following parameters for PC given time using logistic regression: PC_5 ($\beta_0 = 4.11$, $\beta_1 = -0.66$), PC_4 ($\beta_0 = 4.67$, $\beta_1 = -0.26$), PC_3 ($\beta_0 = 158.66$, $\beta_1 = -3.78$), and PC_2 ($\beta_0 = 25.57$, $\beta_1 = -4.43e^8$). Bayes' theorem was used to convert $\Pr\{PC|t\}$ to $\Pr\{t|PC\}$ (Figure 2). There was overlap between PCs 3, 4, and 5, reflecting higher variability in PC for prey items that had

been in the stomach for fewer than 40 hours; however, there was strong separation between PCs 2 and 3 (Figure 2).

Model corroboration

To determine the accuracy of W_i estimates, we compared model predictions to estimates of undigested prey weight generated from a weight-length regression (Figure 3). W_i and regression-based estimates of undigested chum salmon prey weight had a Pearson's correlation coefficient of 0.69 and significant correlation (t-test: $t = 6.79$, $DF = 51$, $P < 0.001$). Over the range of fish sizes sampled, the field-based model had a positive bias, but linear regression indicated convergence at larger chum salmon sizes (Figure 3).

Model application: consumption of chum salmon and other prey

Across all staghorn sculpin, including those with empty stomachs, daily per-capita consumption of chum salmon averaged (±SD) 0.04 $g \cdot d^{-1}$ (±0.31) while consumption of all prey items averaged 1.65 $g \cdot d^{-1}$ (±3.65). Based on a mean juvenile chum salmon weight of 2 grams, this translates to one fiftieth of a chum salmon (0.02) consumed per day by the average staghorn sculpin. For only those staghorn sculpins that consumed chum salmon, daily consumption estimates of juvenile chum salmon ranged from 0.12 $g \cdot d^{-1}$ to 5.51 $g \cdot d^{-1}$, or less than one to nearly three (0.06 to 2.76) individual chum salmon per day. Daily consumption estimates were similar between years for both chum salmon (2016: 0.04 $g \cdot d^{-1}$ ±0.34 & 2017: 0.34 $g \cdot d^{-1}$ ±0.28) and all prey (2016: 1.77 $g \cdot d^{-1}$ ±4.53 & 2017: 1.55 $g \cdot d^{-1}$ ±2.64).

Across years, daily consumption of chum salmon was lower in early May, higher in late May, and lower in early June, although differences were more pronounced in 2017 (Figure 4). Across periods and years, chum salmon were always a minority of prey consumed and no consumption of chum salmon was detected before early May or after early June. Overall,

consumption appeared to be low in April, peaked in late May or early June, and declined slightly through early July. Over the entire period of chum salmon outmigration and hatchery releases (April-June), an individual staghorn sculpin is estimated to consume 3.6 g of juvenile chum salmon, or 1.8 individuals, on average.

Discussion

We determined gastric evacuation rates for staghorn sculpin in the northern portion of their range and applied this information using a field-based model to calculate consumption rates from diet data obtained near Juneau, Alaska, in 2016 and 2017 to investigate predation on juvenile chum salmon. Our results indicate that monthly consumption patterns by staghorn sculpin were consistent across years and follows the pattern of chum salmon availability in the estuary (Duncan, 2018). Although chum salmon were consumed, staghorn sculpin consumption was dominated by other prey groups, indicating that they rely more heavily on invertebrates and other fishes. Although we do not have population estimates for staghorn sculpin in the Juneau area, our consumption model results suggest that it would require more than 722,000 staghorn sculpins consuming an average of 1.8 chum salmon between April and June to remove just 1% of the 130 million chum salmon smolts released by the Douglas Island Pink and Chum Inc. hatchery. While we did not elaborate on the differences between hatchery and wild chum salmon in this paper, it is important to note that wild chum salmon average approximately 1/3 the mass of hatchery -origin chum salmon which means that at the same consumption rate, more wild individuals would be consumed (Duncan, 2018). This study provides new information about early marine mortality of juvenile chum salmon, and new insights into staghorn sculpin feeding ecology including their ability to utilize seasonally pulsed subsides common to estuary habitats.

All consumption models include assumptions and can be subject to biases from multiple sources, so the plausibility of outputs must be assessed (Elliott & Persson, 1978). With our field-based technique, one of the primary assumptions is that the gastric evacuation function is generalizable to all prey types. The high diversity of prey consumed by staghorn sculpin makes it difficult to evaluate the accuracy of outputs for all prey types, but we used a length-weight regression to corroborate W_i estimates for the species of primary interest, chum salmon. We found a significant correlation between W_i and the length-weight regression, with moderately strong agreement in calculated values. All W_i values fell within the range of weights observed for juvenile chum salmon found at study sites. These results suggest that our field-based model yielded plausible estimates of chum salmon consumption by staghorn sculpins. Using a body structure to body size relationship to determine undigested prey weight is not feasible for all prey types in generalist consumer diets, so consumption models remain useful tools. A bioenergetics model has not been parameterized for staghorn sculpin but based on studies showing agreement between bioenergetics models and the form of the field-based model we used here (Beaudreau & Essington 2009, Holsman & Aydin 2015), we expect that bioenergetics-based consumption estimates would be comparable to those reported here. Comparative studies for a wide variety of fish species suggest that bioenergetics models typically yield higher consumption estimates than field-based approaches (Beaudreau & Essington 2009; Chipps & Wahl 2008).

Mace (1983) examined gastric evacuation rates in staghorn sculpin, but under different conditions. Experiments by Mace (1983) were carried out in freshwater, with temperatures ranging from 10 to 17 °C, using staghorn sculpin ranging in length from 50 to 100 mm. In our study, experiments were conducted in saltwater ranging in temperature from 7.3 to 8.2 °C and used staghorn sculpins ranging in length from 144 to 256 mm. Mace (1983) determined the

gastric evacuation function to be best fit by an exponential model and observed more rapid gastric evacuation compared to our results (Figure 5). Neither Mace (1983) nor our study found a significant relationship between predator size and gastric evacuation rate across sampled size classes; however, size distributions of experimental fish did not overlap between the two studies. The metabolic rates of teleosts have been found to increase with the 0.75 power of body mass and exponentially with temperature (Gillooly et al. 2001). Therefore, the difference in evacuation rates may have resulted from the allometry of metabolism, temperature, or both (i.e., faster metabolic rates are expected with smaller fish and warmer temperatures). The substantial difference in temperature between studies was likely responsible for most of the discrepancy in evacuation rate, given the positive relationship between temperature and metabolism of ectotherms (Gillooly et al. 2001). Together, the Mace (1983) study and ours provide a range of gastric evacuation rates for staghorn sculpins under varying thermal conditions.

Staghorn sculpins are documented as having a very broad thermal tolerance range (Morris 1960) and occupy the intertidal zone where large variations in water temperature occur over small areas (Abookire et al. 2000). Mobile fishes may move among thermal regimes to maximize growth potential, such as juvenile coho salmon (*O. kisutch*) that foraged in cold river channels at night and moved into warmer off-channel habitats during the day to increase digestion rates (Baldock et al. 2016). It is possible that staghorn sculpin may also move to optimize their thermal environment, which could result in different gastric evacuation rates in the wild than observed in laboratory fish. If staghorn sculpins are moving to warmer waters to digest more quickly, then it could explain the high incidences of stomachs with prey (~99%) collected in beach seines. A bias towards sampling individuals with higher than representative stomach contents would create a positive bias in consumption rate calculations. However, we expect that

the temperatures in which we collected staghorn sculpins were largely representative of their summer thermal experience, as our beach seine sampling occurred in intermediate temperatures in the Lynn Canal area (approximately 5-13°C, May-July; unpublished data).

In some fish species, gastric evacuation rates observed in single meal, single prey type feeding trials may not be representative of digestive rates under natural feeding regimes (Bromley 1994), but Mace (1983) found that gastric evacuation rate in staghorn sculpin did not change significantly with mixed fish and small invertebrate rations. We did not evaluate the impact of multiple feedings or prey types on gastric evacuation rates, but these results from Mace (1983) support the generalizability of gastric evacuation rates across prey types for staghorn sculpins. This is important because staghorn sculpin are opportunistic consumers with diverse diets that include fish and invertebrate prey (Whitney et al. 2017).

Conclusions

Staghorn sculpins are a common generalist consumer found in estuaries along the west coast of North America. Despite their prevalence, little is known about their life history or ecology. By determining their gastric evacuation rate and demonstrating application of a field-based consumption model, we have contributed to knowledge about the ecology of staghorn sculpin and generated a tool to more easily evaluate their ecological role in other coastal regions. The field-based model application, corroborated with a regression-based estimator, also gives hatchery operators and managers a new method to evaluate the potential scope for predation on juvenile salmon by staghorn sculpin near Juneau, Alaska. Although our results suggest that staghorn sculpins may remove only a minor fraction of hatchery released fish, their predatory impact may vary in space and time. More generally, these consumption estimates allow for a

better understanding of energy flows through nearshore habitats that serve as nurseries for a wide range of organisms and are subject to anthropogenic development and disturbance.

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Figures

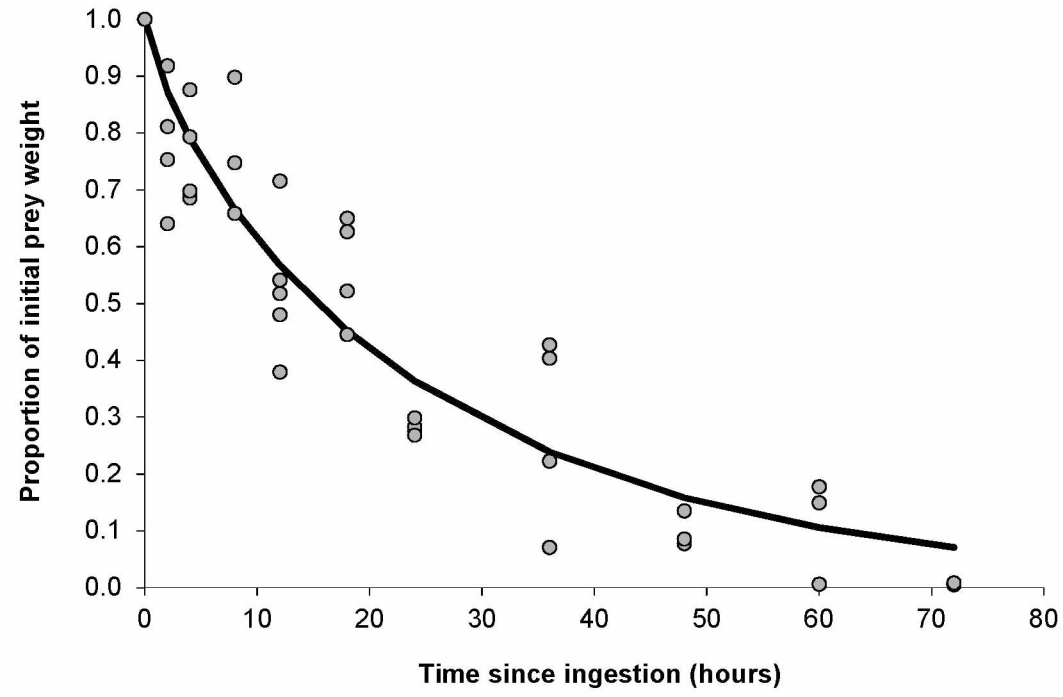

Figure 2.1 Staghorn sculpin gastric evacuation data fitted with the best-fit sigmoid model. Each point represents an individual feeding trial.

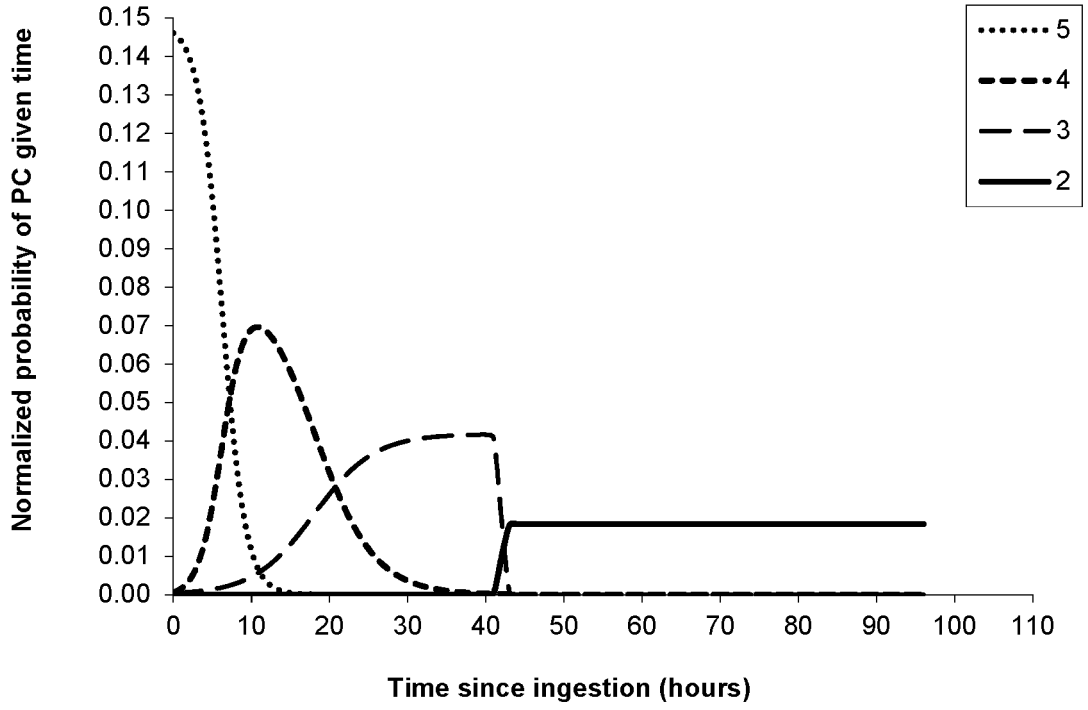

Figure 2.2 Probabilities of time since ingestion given observed prey condition (PC) codes, ranging PC 5 (little digestion) to PC 2 (near complete digestion).

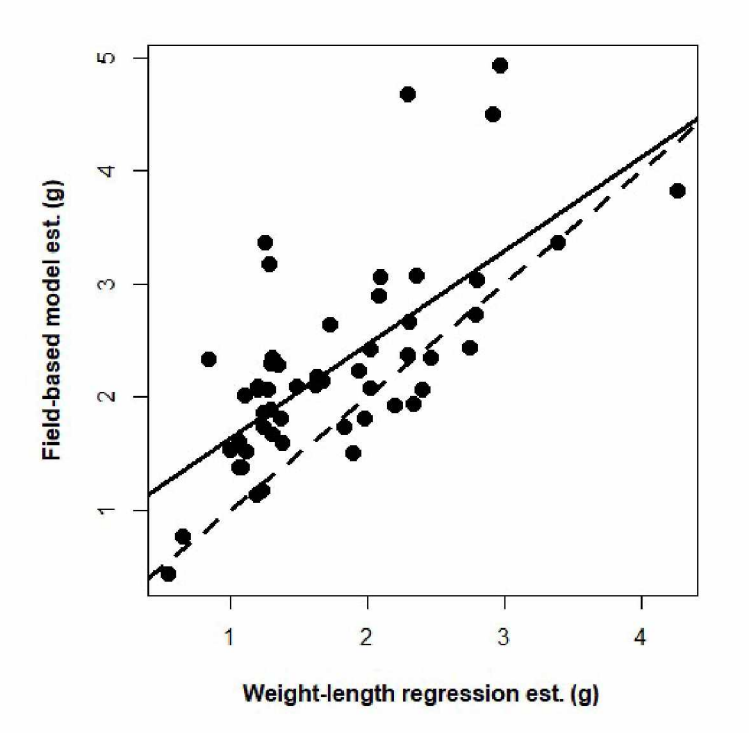

Figure 2.3 Comparison of estimated chum salmon weight consumed by staghorn sculpins from a field-based consumption model and a length-weight regression. The dashed line is a 1:1 line and the solid line is a linear regression between W_i estimates generated by the weight-length regression model and those generated by the field-based consumption model to visualize trends.

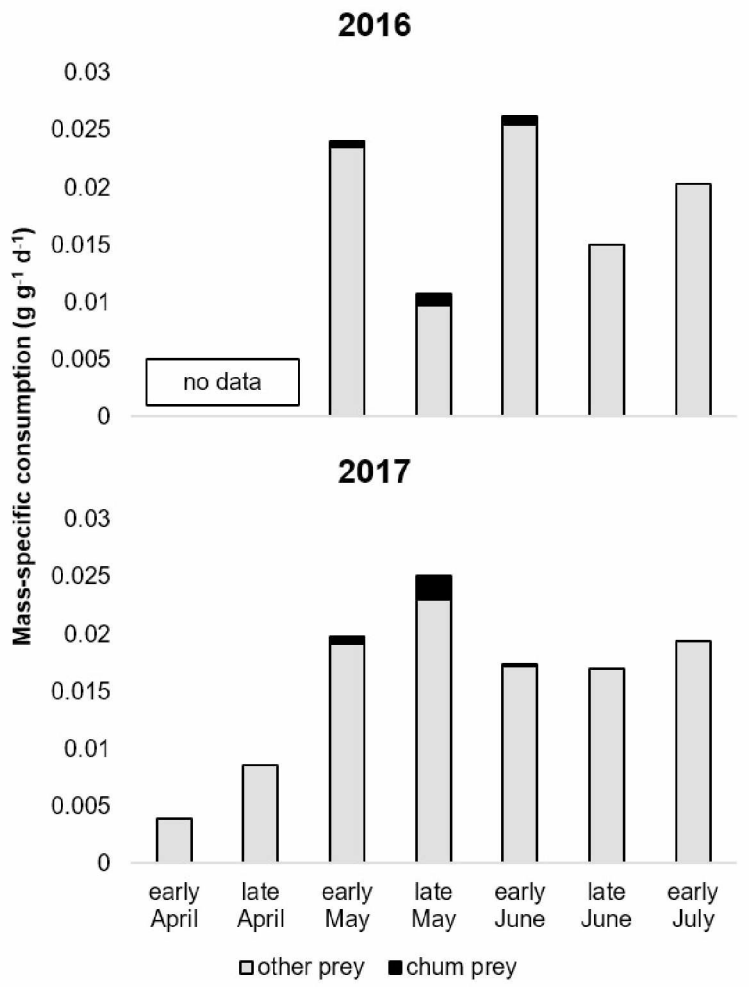

Figure 2.4 Mass-specific per capita consumption estimated by the field-based model at each sampling period.

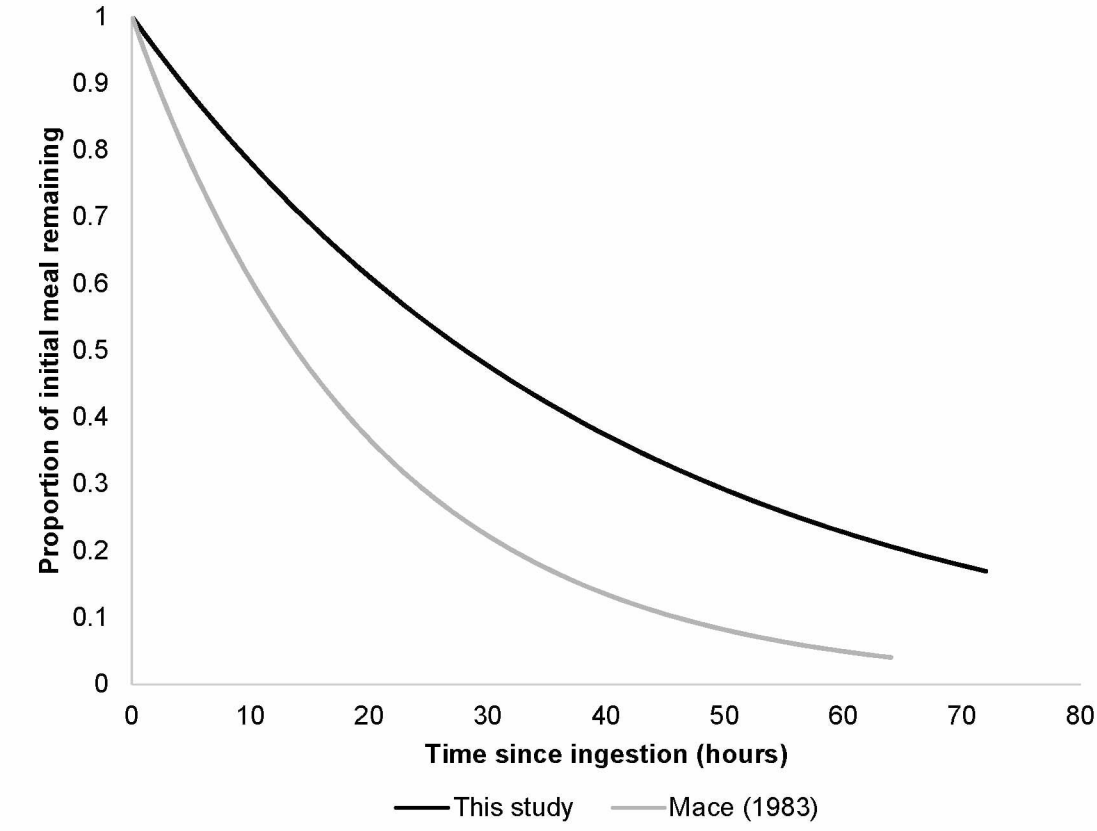

Figure 2.5 Gastric evacuation functions determined for staghorn sculpin by our study and Mace (1983) with experimental feeding trails.

Tables

Table 2.1 Model form and AIC values for candidate models describing gastric evacuation, where P is the proportion of prey remaining, t is time since ingestion in hours, and β_n are estimated coefficients of the models.

Model type	Function	AIC	ΔAIC
Sigmoid	$P = 1 - [1 - \exp(-\beta_0 t)]^{\beta_1}$	-164.4	0.0
Power exponential	$P = 2^{-(\frac{t}{\beta_0})^{\beta_1}}$	-162.8	1.6
Exponential	$P = \beta_0 \exp(-\beta_1 t)$	-159.7	4.7
Square root	$P = {\beta_0}^2 - 2\beta_0\beta_1 t + (\beta_1 t)^2$	-144.7	19.7
Gompertz	$P = 100 - \beta_0 \exp[\beta_1 \exp(\beta_2 t)]$	-134.8	29.7
Logistic	$P = 100 - \frac{\beta_0}{1 + \exp[\beta_1(t + \beta_2 t)]}$	-119.7	44.7
Logistic restricted	$P = 100 - \frac{100}{1+\exp[\beta_0(t+\beta_1)]}$	-107.2	57.2
Linear	$P = \beta_0 - \beta_1 t$	-84.7	79.7

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General Conclusions

Chapter 1

Contribution of chum salmon prey to predator diets

Pacific staghorn sculpin and Dolly Varden are two prevalent consumers in estuaries near Juneau, AK, that overlap with juvenile salmon during their high mortality marine entry phase and are known to take advantage of seasonally pulsed prey resources (Roos 1959; Whitney et al. 2017). We examined the diets of predators in estuaries from May to July of 2016 and April to July of 2017 and found that 4.5% of staghorn sculpin diets by weight consisted of juvenile chum salmon and that this prey item occurred in 3.3% of sampled individuals. For Dolly Varden, chum salmon made up 19.6% of the diet by weight and occurred in 10.0% of sampled individuals. This indicates that per capita, Dolly Varden consume more chum salmon prey than staghorn sculpin. However, determining the total consumption by each predator species requires information about both consumption rates and population sizes. Predator population sizes are largely unknown, but there is a robust recreational fishery for Dolly Varden near hatchery release sites that may be a source of local removals while staghorn sculpins are not harvested at all.

Size- and origin-based patterns of predation

Chum salmon consumed by both predators were smaller on average than chum salmon captured concurrently in beach seines or released from the hatchery, and were mostly of hatchery origin. This may indicate a preference for smaller fish, which would be consistent with studies of many other piscivorous fishes (Healey 1982, Juanes 1994, Sogard 1997, Duffy & Beauchamp 2008). Apparent selectivity for smaller juvenile chum salmon also supports the hatchery strategy of releasing larger individuals to increase survival at this stage. However, it is important to recognize the potential for countervailing selection later in life that might diminish these

benefits. First, it has been found that rapid early growth in chum salmon, as with other salmonids, can lead to smaller and younger returning adults (Morita et al. 2005), which is consistent with findings of mature hatchery-born chum salmon adults being smaller than wild-born individuals (McConnell et al. 2018). Additionally, holding chum salmon for longer periods can change timing and migration patterns (Sturdevant et al., 2012) which may lead to mismatch with food resources or possibly match conditions with predators. Both smaller returning adults and decreased survival (adult abundance), or increased variability, run contrary to fisheries enhancement goals. When comparing predation on hatchery- and wild-born chum salmon, we found that 88% of chum salmon in predator stomachs were of hatchery origin. This closely matches the proportion of hatchery- and wild-born fish in concurrent beach seine samples when chum salmon abundances were high, suggesting that patterns of predation may mirror relative densities of hatchery- and wild-born fish. As the smolt to adult survival or hatchery origin salmon has been found to be lower than wild-born individuals (Kostow 2004), the proportionally equal predation may have the potential be significant for wild-born stocks.

Spatial and temporal patterns of predation

We found strong seasonal patterns in beach seine catches and the presence of chum salmon in predator diets. Salmon were less abundant in April, peaked in abundance from May to early June, and declined in abundance for the rest of our sampling through the beginning of July. The proportion of salmon in diets largely followed these trends. As the predators that we sampled are generalists, it is expected that more chum salmon were incorporated into their diets when chum salmon CPUE was higher, which is likely a function of increased prey encounter rates (Juanes et al. 2008). Spatially, the contribution of salmon to predator diets was also higher

at sites with higher average chum salmon CPUE, specifically Mendenhall River and Sheep Creek, which were directly in the path of juvenile chum salmon leaving hatchery release sites.

Factors explaining variation in predation of chum salmon

We statistically evaluated predictors of chum salmon occurrence in diets and found that site and day of year were indicated as most important. Day of year is intuitive, as consumption by both predators is ultimately delineated by the relatively short, seasonal residency period of juvenile chum salmon in estuary habitats (Quinn 2005). Site is a more difficult covariate to clearly interpret as it is confounded with other variables including CPUE, distance from hatchery release, bathymetry, and other unmeasured habitat or environmental variables. The sites where most consumption of salmon occurred had higher average juvenile chum salmon CPUE, driven by hatchery origin chum salmon. Not only were hatchery origin chum salmon found in much higher densities than wild-born fish, but they were larger, had better condition factors, and were likely more behaviorally vulnerable to predators (Olla et al. 1998).

The best predictors of the standardized mass of chum salmon prey for staghorn sculpin were the proportion of hatchery origin chum present during sampling, predator length, and juvenile chum salmon CPUE. Chum salmon CPUE is likely an important driver of the quantity of chum salmon consumed by staghorn sculpin because they are sedentary ambush predators (Tasto 1975). As we never encountered CPUEs of wild-born chum salmon that equaled those found for hatchery origin chum salmon, it is difficult to know whether increased predation was a density dependent function, related to differences between hatchery- and wild-born chum salmon, or resulted from some combination of factors. Finding a comparable site with no hatchery input and evaluating predator diets would provide much insight into how hatcheries may be altering food webs. For Dolly Varden, day of year was the only strong predictor of

quantity. This may reflect differences in the mobility of predators, with Dolly Varden being seasonally migratory, mobile (Armstrong 1970) and potentially better at tracking prey independent of local availability.

The results from this chapter are consistent with results from other studies examining predation on juvenile salmon, which have generally found that salmon were not the dominant component of predator diets (Roos 1959, Mace 1983, Whitney et al. 2017). During spring and summer, there are multiple overlapping prey resource pulses in Southeast Alaska estuaries, including Pacific herring (*Clupea pallasii*), Pacific sand lance (*Ammodytes hexapterus*), smelts (Osmeridae spp.), and invertebrates which we found constituted a larger part of predator diets compared to juvenile chum salmon. Much of the early marine mortality on salmon remains poorly explained. Either a wider assessment of potential predators is still required, or the mortality rates from currently documented sources must be evaluated in wholistic manner to better explain the mechanisms driving this mortality.

Chapter 2

Gastric evacuation rate of staghorn sculpin

Diet data provide a snapshot of predator diets, but information about consumption rates is needed to quantify food intake over time. We found that it took staghorn sculpins approximately 72 hours to fully digest a single salmon smolt under experimental conditions representative of study sites. A sigmoidal function was determined to best describe gastric evacuation and allowed us to calculate the probabilistic relationship between time and prey condition. Knowing how long it took an item to reach a specified level of digestion in the stomach allowed us to estimate the initial weight of the prey with a field-based consumption model. With this information, we were able to calculate daily consumption for staghorn sculpin. With the addition of this study, gastric

evacuation rates are known for staghorn sculpin in warm freshwater (Mace 1983) and colder estuary conditions, which gives researchers tools to evaluate consumption under multiple conditions.

Field-based consumption model corroboration

We corroborated the field-based consumption model estimates using a length-weight relationship determined for chum salmon sampled at study sites. We found that the two methods had a significant positive relationship, with the field-based method having a positive bias but producing reasonable results. All field-based model outputs fell within the range of chum salmon weights observed in beach seine catches, suggesting our model results were realistic.

Field-based model application: consumption of salmon

To assess the cumulative seasonal consumption of chum salmon by staghorn sculpin, we applied our field-based consumption model to the diet data from Chapter 1. From this we estimated daily individual and mass-specific consumption of staghorn sculpin. Individual sculpins that incorporated juvenile chum salmon into their diet were estimated to consume between less than one to nearly three hatchery origin or six wild-born chum salmon per day. Average consumption of chum salmon was much lower; our results suggest it would take a staghorn sculpin population of more than 700,000 to consume just 1% of the annual chum salmon production from DIPAC. While we do not have population estimates for staghorn sculpin, it seems improbable that the millions of staghorn sculpins required to consume an appreciable quantity of staghorn sculpin exist in the constrained areas near DIPAC's hatchery release sites. Another important unknown is the amount of natural chum salmon production that occurs at the study sites, and if relatively few removals may be harmful when compared to a robust hatchery population.

To definitively evaluate impact of staghorn sculpin predation on juvenile chum salmon, predator population sizes and an understanding of what level of mortality would be required to result in a clear difference in the number of returning adults must be known. What the diet data and consumption estimates do tell us is that on average chum salmon were always a minority of the prey consumed by staghorn sculpins, and that other abundant prey resources in estuaries, not chum salmon, were a majority of the prey consumed. If these other estuary food resources are reduced because of human development or climate change, it may be reasonable to expect more predation on juvenile salmon by these generalist predators.

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Appendices

Appendix A Sample sizes and mean standard lengths (±standard deviation) of juvenile chum salmon subsampled from beach seine catches to determine proportion of hatchery origin fish. Asterisk denotes that all juvenile chum salmon captured that sampling day were assessed for origin. ER = Eagle River, CC = Cowee Creek, MR = Mendenhall River, SC = Sheep Creek

		Sampling period								
		early May				late May				early June
		ER	CC	MR	SC	ER	CC	MR	SC	MR
2016	prop. marked	0	n/a	1	1	0.85	0.9	0.85	1	0.95
	count	3*	0*	20	20	20	20	20	20	20
	hatchery-born mean length ± SD (mm)	n/a	n/a	55.1 (±5.0)	61.7 (±3.3)	54.6 (±10.6)	69.2 (±7.8)	55.8 (±5.2)	56.4 (±7.5)	62.7 (±9.1)
	wild-born mean length ± SD (mm)	57.4 (±6.3)	n/a	n/a	n/a	49.0 (±13.2)	57.0 (±5.7)	51.2 (±2.9)	n/a	61.0 (±0.0)
2017	prop. marked	0	0	0	0.15	1	0.8	0.95	0.85	n/a
	count	20	1*	20	20	18	20	20	20	n/a
	hatchery-born mean length ± SD (mm)	n/a	n/a	n/a	50.0 (±2.0)	64.2 (±8.0)	63.7 (±6.5)	65.4 (±4.9)	54.1 (±3.8)	n/a
	wild-born mean length ± SD (mm)	38.1 (±4.0)	46 (±0.0)	38.0 (±5.0)	35.6 (±2.6)	n/a	50.0 (±7.7)	44.0 (±0.0)	46.3 (±4.7)	n/a

Appendix B Percent weight (Wi) and frequency of occurrence (Oi) of prey groups for Pacific staghorn sculpins and Dolly Varden across seven sampling periods in 2016-2017.

(a) Pacific staghorn sculpin

	May 2016		Jun 2016		Jul 2016		Apr 2017		May 2017		Jun 2017		Jul 2017		Overall	
	Wi	**Oi**	**Wi**	**Oi**	**Wi**	**Oi**	**Wi**	**Oi**	**Wi**	**Oi**	**Wi**	**Oi**	**Wi**	**Oi**	**Wi**	**Oi**
Juvenile salmon																
Chum salmon	9.6%	8.0%	4.5%	2.2%	0.0%	0.0%	0.0%	0.0%	10.2%	8.1%	0.9%	1.3%	0.0%	0.0%	4.5%	2.8%
Coho salmon	8.7%	3.4%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	3.3%	0.7%	0.0%	0.0%	0.0%	0.0%	2.0%	0.4%
Salmon unid.	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.1%	0.4%	0.0%	0.0%	0.0%	0.1%
Other fishes																
Pacific herring	9.0%	2.3%	2.5%	2.2%	14.0%	4.9%	0.0%	0.0%	21.0%	11.8%	17.3%	6.9%	18.6%	6.5%	13.2%	5.6%
Pacific sand lance	13.4%	5.7%	10.0%	9.5%	20.9%	27.0%	33.4%	28.6%	22.9%	11.0%	14.1%	9.1%	1.2%	4.1%	14.5%	11.0%
Cottidae	5.7%	9.2%	6.8%	16.5%	2.1%	3.3%	0.0%	0.0%	0.0%	0.7%	0.0%	0.0%	0.1%	0.8%	2.6%	5.5%
Osmeridae	0.3%	1.1%	0.0%	0.0%	7.0%	4.1%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	1.0%	0.6%
Pleuronectiformes	8.8%	9.2%	11.7%	13.0%	2.1%	9.0%	0.0%	0.0%	0.2%	1.5%	4.2%	3.0%	3.6%	7.3%	5.4%	7.1%
Stichaeidae	1.5%	9.2%	5.0%	14.3%	1.9%	1.6%	0.0%	0.0%	9.6%	0.7%	0.3%	1.7%	0.6%	2.4%	3.5%	5.4%
Other teleost	0.0%	0.0%	1.8%	6.9%	0.2%	2.5%	0.0%	0.0%	0.7%	2.2%	0.0%	0.4%	0.0%	0.0%	0.5%	2.4%
Teleost adult scavange	2.1%	1.1%	4.9%	0.9%	0.0%	0.0%	0.0%	0.0%	1.9%	0.7%	0.0%	0.0%	5.6%	1.6%	2.3%	0.6%
Teleost, unid.	5.2%	33.3%	11.2%	53.2%	15.4%	50.8%	1.6%	28.6%	8.8%	34.6%	9.5%	35.9%	4.6%	21.1%	9.3%	39.6%
Invertebrates																
Amphipod	1.6%	42.5%	5.4%	72.7%	3.2%	76.2%	0.8%	28.6%	1.8%	48.5%	2.4%	42.4%	3.7%	62.6%	3.0%	57.6%
Annelida	9.9%	54.0%	9.3%	50.6%	6.2%	47.5%	40.6%	42.9%	4.5%	45.6%	11.8%	37.7%	5.1%	35.8%	8.3%	44.5%
Bivalve	0.1%	8.0%	1.9%	15.2%	0.2%	16.4%	5.5%	28.6%	0.0%	8.1%	0.4%	20.8%	0.9%	37.4%	0.7%	18.0%
Pleocyemata	8.5%	29.9%	6.8%	26.4%	2.3%	14.8%	15.7%	28.6%	3.5%	10.3%	10.0%	27.3%	6.3%	26.8%	6.5%	23.1%
Malacostraca	2.8%	26.4%	3.2%	40.3%	1.8%	47.5%	1.2%	14.3%	0.7%	16.2%	1.4%	12.6%	0.8%	20.3%	1.9%	26.7%
Isopod	4.6%	39.1%	9.2%	57.6%	14.4%	63.1%	0.0%	0.0%	3.7%	51.5%	19.3%	64.1%	37.7%	74.0%	13.1%	58.8%
Crustacean	1.6%	25.3%	4.3%	41.6%	6.4%	49.2%	1.2%	42.9%	2.1%	39.7%	3.7%	38.5%	4.8%	44.7%	3.7%	40.3%
Other invertebrates	2.6%	23.0%	0.5%	34.2%	0.2%	31.1%	0.0%	0.0%	0.7%	29.4%	0.7%	35.1%	1.2%	41.5%	0.9%	32.7%

Eggs																
Salmon eggs	0.0%	0.0%	0.0%	0.0%	1.4%	1.6%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.2%	3.3%	0.2%	0.6%
Eggs, unid.	3.9%	1.1%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	3.2%	2.2%	0.0%	0.0%	0.0%	0.0%	1.2%	0.4%
Other																
Tissue, unid.	0.2%	9.2%	0.7%	13.9%	0.4%	3.3%	0.0%	0.0%	0.9%	8.1%	3.8%	6.9%	4.9%	11.4%	1.7%	9.0%
Empty	0.0%	2.3%	0.0%	0.9%	0.0%	0.0%	0.0%	0.0%	0.0%	1.5%	0.0%	0.9%	0.0%	0.8%	0.0%	1.0%

(b) Dolly Varden

	May_16		Jun_16		Jul_16		Apr_17		May_17		Jun_17		Jul_17		Overall	
	Wi	**Oi**	**Wi**	**Oi**	**Wi**	**Oi**	**Wi**	**Oi**	**Wi**	**Oi**	**Wi**	**Oi**	**Wi**	**Oi**	**Wi**	**Oi**
Juvenile salmon																
Chum salmon	28.4%	15.1%	0.4%	0.8%	0.0%	0.0%	4.3%	15.6%	16.1%	4.5%	45.0%	18.1%	0.0%	0.0%	19.6%	8.9%
Coho salmon	39.7%	1.4%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	31.2%	2.3%	0.0%	0.0%	0.0%	0.0%	15.0%	0.4%
Salmon unid.	0.7%	4.1%	0.1%	0.8%	1.9%	7.7%	0.0%	0.0%	0.0%	0.0%	0.2%	0.9%	0.0%	0.0%	0.3%	1.3%
Other fishes																
Pacific Herring	7.2%	6.8%	13.7%	1.5%	0.0%	0.0%	0.0%	0.0%	6.7%	2.3%	7.8%	3.4%	0.0%	2.5%	8.0%	2.9%
Pacific Sand Lance	1.7%	5.5%	34.3%	43.8%	13.7%	15.4%	72.8%	37.5%	1.7%	2.3%	29.8%	24.1%	15.9%	15.0%	22.3%	24.6%
Pleuronectiformes	0.0%	1.4%	0.0%	1.5%	3.3%	23.1%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.1%	1.3%
Stichaeidae	0.0%	0.0%	14.1%	13.1%	0.0%	0.0%	0.3%	3.1%	0.6%	2.3%	0.5%	1.7%	3.0%	5.0%	4.2%	5.1%
Agonidae	4.5%	19.2%	0.5%	7.7%	0.0%	0.0%	0.0%	0.0%	3.8%	4.5%	0.0%	1.7%	0.0%	0.0%	1.8%	6.3%
Pholidae	0.0%	0.0%	1.9%	16.9%	0.0%	0.0%	0.6%	3.1%	0.0%	0.0%	0.1%	1.7%	0.0%	0.0%	0.6%	5.6%
Cottidae	0.2%	12.3%	0.4%	11.5%	0.0%	0.0%	6.5%	34.4%	0.0%	0.0%	0.0%	0.9%	0.0%	0.0%	0.7%	8.0%
Other teleost	0.0%	0.0%	0.0%	0.0%	0.2%	7.7%	0.0%	0.0%	0.0%	0.0%	0.7%	0.9%	0.0%	0.0%	0.1%	0.4%
Teleost, unid.	2.8%	26.0%	1.0%	26.9%	5.5%	46.2%	0.5%	18.8%	0.2%	9.1%	2.0%	15.5%	0.1%	10.0%	1.8%	20.5%
Invertebrates																
Polychaeta	0.8%	9.6%	0.1%	9.2%	0.0%	0.0%	2.1%	21.9%	0.2%	2.3%	0.2%	4.3%	0.1%	5.0%	0.5%	7.6%
Amphipod	8.1%	64.4%	23.9%	78.5%	42.7%	76.9%	8.7%	65.6%	19.2%	70.5%	3.5%	41.4%	4.7%	65.0%	12.3%	63.6%
Pleocyemata	0.2%	6.8%	0.0%	4.6%	0.7%	15.4%	0.0%	0.0%	0.1%	6.8%	0.0%	0.9%	0.0%	0.0%	0.1%	3.8%
Malacostraca	0.1%	4.1%	2.6%	45.4%	7.9%	61.5%	2.4%	37.5%	1.6%	9.1%	0.4%	10.3%	0.5%	27.5%	1.2%	24.3%
Crustacean	0.6%	11.0%	0.3%	6.9%	2.6%	23.1%	0.2%	18.8%	8.9%	45.5%	0.4%	7.8%	1.4%	27.5%	0.9%	14.7%
Insect	0.1%	17.8%	0.7%	44.6%	0.3%	15.4%	0.2%	21.9%	2.4%	50.0%	4.9%	44.0%	3.2%	70.0%	1.5%	40.4%
Copepod	0.6%	17.8%	0.1%	15.4%	0.0%	0.0%	0.0%	0.0%	1.7%	36.4%	1.1%	24.1%	0.1%	12.5%	0.5%	18.3%

Cumacean	4.0%	46.6%	4.8%	69.2%	6.3%	61.5%	0.5%	28.1%	4.8%	72.7%	2.8%	49.1%	8.5%	70.0%	4.1%	57.6%
Isopod	0.3%	5.5%	0.9%	21.5%	3.0%	38.5%	0.1%	9.4%	0.4%	15.9%	0.4%	15.5%	5.8%	27.5%	0.8%	17.0%
Other invertebrates	0.0%	5.5%	0.1%	10.8%	0.0%	0.0%	0.1%	9.4%	0.1%	6.8%	0.2%	14.7%	2.1%	42.5%	0.2%	12.9%
Eggs																
Salmon eggs	0.0%	0.0%	0.0%	0.0%	11.8%	7.7%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	54.1%	22.5%	3.4%	2.2%
Eggs, unid.	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.3%	6.3%	0.0%	0.0%	0.0%	1.7%	0.0%	0.0%	0.0%	0.9%
Other																
Unknown Tissue	0.1%	16.4%	0.0%	2.3%	0.0%	0.0%	0.2%	12.5%	0.0%	2.3%	0.0%	3.4%	0.5%	5.0%	0.1%	5.8%
Empty	0.0%	5.5%	0.0%	0.8%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.9%	0.0%	0.0%	0.0%	1.3%

Appendix C Model coefficient estimates for logistic regression on occurrence (presence/absence) of chum salmon in (a) Pacific staghorn sculpin stomachs (n=928), and (b) Dolly Varden stomachs (n=442).

Model	Model coefficients								K	AICc
	intercept	site: ER	site: MR	site: SC	year: 2017	day of year	chum CPUE	predator length		
(a) Pacific staghorn sculpin										
1	3.916	-2.607	0.052	-0.205	NA	-0.059	0.009	0.009	8	190.4
2	5.749	-2.190	0.400	-0.118	NA	-0.061	0.008	NA	7	191.2
3	4.330	-2.685	-0.172	-0.161	-0.397	-0.060	0.010	0.008	9	191.9
4	6.225	-2.311	0.137	-0.063	-0.495	-0.062	0.010	NA	8	192.2
5	4.021	NA	NA	NA	NA	-0.052	0.012	NA	4	193.6
6	2.319	NA	NA	NA	NA	-0.049	0.013	0.006	5	194.2
(b) Dolly Varden										
1	3.448	-0.147	1.473	3.125	1.645	-0.062	0.029	NA	8	128.2
2	2.845	-0.164	1.491	3.095	1.640	-0.060	0.029	0.001	9	130.3
3	6.380	-0.145	0.518	3.311	NA	-0.076	0.035	NA	7	132.2
4	5.410	-0.124	0.566	3.282	NA	-0.071	0.035	0.002	8	134.1
5	-7.459	0.457	1.679	2.190	1.650	NA	0.032	0.009	8	138.7
6	0.309	NA	NA	NA	1.639	-0.035	0.048	NA	5	139.6

Appendix D Appendix Table 3: Model summaries for linear regression on the standardized mass of chum salmon prey in (a) Pacific staghorn sculpin stomachs (n=26), and (b) Dolly Varden stomachs (n=40). 64 models were evaluated for staghorn sculpin with all combinations of the following predictors: site (factor), day of year, chum CPUE, year (factor), predator length, and proportion of hatchery chum present in seine catches (hatchery prop.). 32 models were evaluated for Dolly Varden with all combinations of the following predictors: site (factor), day of year, chum CPUE, year (factor), and predator length. K indicates the total number of parameters estimated and AICc is Akaike's information criteria, bias-corrected for small sample size.

Model	**Model coefficients**									**K**	**AICc**
	intercept	site: ER	site: MR	site: SC	year: 2017	day of year	chum CPUE	predator length	hatchery prop.		
(a) Pacific staghorn sculpin											
1	-1.291	NA	NA	NA	NA	NA	NA	-0.014	1.939	4	54.2
2	-1.782	NA	NA	NA	NA	NA	0.005	-0.009	0.700	5	54.8
3	-2.980	NA	NA	NA	NA	NA	0.009	NA	-0.632	4	55.2
4	-1.638	NA	NA	NA	0.218	NA	NA	-0.013	1.961	5	57.9
5	0.262	NA	NA	NA	NA	-0.011	NA	-0.014	2.119	5	58.1
6	2.732	NA	NA	NA	NA	-0.033	0.006	-0.010	1.053	6	58.5
(b) Dolly Varden											
1	-0.467	NA	NA	NA	NA	0.005	NA	NA		3	-55.5
2	-0.448	NA	NA	NA	0.038	0.005	NA	NA		4	-53.9
3	-0.373	NA	NA	NA	NA	0.005	NA	-0.000		4	-53.5
4	-0.429	NA	NA	NA	0.034	0.005	NA	-0.000		5	-51.3
5	-0.404	-0.033	-0.005	0.004	NA	0.005	NA	NA		6	-47.7
6	0.328	-0.094	-0.029	0.109	NA	NA	NA	-0.001		6	-47.7

Appendix E 2016 IACUC approval letter

(907) 474-7800
(907) 474-5989 fax
iacuc-admin@alaska.edu
www.rcdr.uaf.edu/iacuc

Institutional Animal Care and Use Committee

909 N Koyukuk Dr. Suite 212, P.O. Box 757270, Fairbanks, Alaska 99775-7270

April 29, 2016

To: Anne Beaudreau
Principal Investigator

From: University of Alaska Fairbanks IACUC

Re: [880562-2] Navigating the predator gauntlet: Impacts of nearshore marine fishes on hatchery and wild juvenile salmon in Southeast Alaska

The IACUC reviewed and approved the Revision to the Personnel List referenced above by Administrative Review.

Received:	April 28, 2016
Approval Date:	April 29, 2016
Initial Approval Date:	April 14, 2016
Expiration Date:	April 14, 2017

This action is included on the May 12, 2016 IACUC Agenda.

PI responsibilities:

- *Acquire and maintain all necessary permits and permissions prior to beginning work on this protocol. Failure to obtain or maintain valid permits is considered a violation of an IACUC protocol and could result in revocation of IACUC approval.*
- *Ensure the protocol is up-to-date and submit modifications to the IACUC when necessary (see form 006 "Significant changes requiring IACUC review" in the IRBNet Forms and Templates)*
- *Inform research personnel that only activities described in the approved IACUC protocol can be performed. Ensure personnel have been appropriately trained to perform their duties.*
- *Be aware of status of other packages in IRBNet; this approval only applies to this package and the documents it contains; it does not imply approval for other revisions or renewals you may have submitted to the IACUC previously.*
- *Ensure animal research personnel are aware of the reporting procedures on the following page.*

Appendix F 2017 IACUC approval letter

(907) 474-7800
(907) 474-5993 fax
uaf-iacuc@alaska.edu
www.uaf.edu/iacuc

Institutional Animal Care and Use Committee

909 N Koyukuk Dr. Suite 212, P.O. Box 757270, Fairbanks, Alaska 99775-7270

July 25, 2017

To: Anne Beaudreau
Principal Investigator

From: University of Alaska Fairbanks IACUC

Re: [880562-9] Navigating the predator gauntlet: Impacts of nearshore marine fishes on hatchery and wild juvenile salmon in Southeast Alaska

The IACUC reviewed and approved the Amendment/Modification referenced above by Designated Member Review.

Received:	July 21, 2017
Approval Date:	July 25, 2017
Initial Approval Date:	April 14, 2016
Expiration Date:	April 14, 2019

This action is included on the August 10, 2017 IACUC Agenda.

PI responsibilities:

- *Acquire and maintain all necessary permits and permissions prior to beginning work on this protocol. Failure to obtain or maintain valid permits is considered a violation of an IACUC protocol and could result in revocation of IACUC approval.*
- *Ensure the protocol is up-to-date and submit modifications to the IACUC when necessary (see form 006 "Significant changes requiring IACUC review" in the IRBNet Forms and Templates).*
- *Inform research personnel that only activities described in the approved IACUC protocol can be performed. Ensure personnel have been appropriately trained to perform their duties.*
- *Be aware of status of other packages in IRBNet; this approval only applies to this package and the documents it contains; it does not imply approval for other revisions or renewals you may have submitted to the IACUC previously.*
- *Ensure animal research personnel are aware of the reporting procedures on the following page.*